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The Hyoid and Its Associated Muscles in Snakes

DAVID A. LANGEBARTEL

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INTRODUCTION

This study has been made to further the knowledge of variation in the hyoid apparatus in snakes, to make known the differences in the musculature associated anatomically and functionally with the hyoid, and to correlate these findings phylogenetically.

The form of the hyoid has been known in a few snakes since the first third of the nineteenth century (Losana, 1832; and d'Alton, 1834). A few other papers treated the subject in subsequent years, but it was not until well over a century after Losana's and d'Alton's works, in 1948, that any extensive study on the variation of the structure was published. In that year Smith and Warner published their findings to establish at once both a remarkable constancy of general hyoid morphology within apparently phyletically related familial groups, and a variability of minor points of the morphology on the generic level.

This author undertook with Smith the project of augmenting the number of snake genera examined for the hyoid. The work was then put aside until some years later, when the author continued it, and also added to it a study of the musculature of the hyoid; the entire work was then offered as a thesis for the Ph.D. degree in zoology at the University of Illinois. Since the completion of the thesis, the entire work has been rewritten, new data added, and the literature brought up to date.

The word "hyoid" is used in this work to denote the total tongue

skeleton. Other words found in the literature referring to this structure are the "hyobranchium" and "hyoglossum."

The hyoid is usually easy to find in most species, lying close to the skin, and only partly covered by muscles. However, in the species of the typhlopidae and leptotyphlopidae snakes, the structure is buried in muscles and therefore not so easy to find without careful dissection.

Anatomists have more actively studied the associated musculature of the hyoid in vertebrates than the structure itself. This is also true for snakes, and the beginning of myological investigation again dates back to the first third of the past century (Dugès, 1827; Duvernoy, 1832; and d'Alton, 1834). It is interesting to note that d'Alton's 1834 essay on the python's muscles is remarkably more accurate than a great number of works which followed his — even of this century. The most research on these muscles in snakes has been done by German anatomists.

Difficulties in muscle dissection are caused by distorted specimens, and by the length of time the specimens have been preserved. Long preservation, particularly in alcohol, softens muscles and causes them to fray and break easily upon dissection.

One reason the ventral head musculature of snakes has been so often incompletely or incorrectly illustrated in the past is that the cutaneous layer has not been recognized or shown. This muscle is very easily destroyed or disarranged upon dissection or even in skinning the head.

The drawings of the muscles were executed by the author and are somewhat diagrammatic.

The following family classification is used in this work:

Anomalepididae
Typhlopidae
Leptotyphlopidae
Uropeltidae
Aniliidae
Xenopeltidae
Boidae
Colubridae
Elapidae
Hydrophidae
Viperidae
Crotalidae

The families Boidae and Colubridae are taken in their broadest sense.

Of this list nearly every genus in all families save the Colubridae

has been examined for the hyoid. Of the colubrids probably a fourth of the genera have been examined. Fewer genera in most families have been dissected for musculature. Several rare genera would have been very desirable to investigate. The east Indian *Anomalochilus*, presumably an aniliid, is one; two others, *Casarea* and *Bolyeria*, are puzzling boidlike forms found on several islands in the Indian Ocean. Fortunately, Anthony and Guibé of the Paris Museum have examined these boids for the hyoid at least and have published their results (1952).

PART I. THE HYOID APPARATUS

A. General Anatomy

The hyoid apparatus in snakes is in several morphological patterns, depending upon the family; it is, in all cases, simplified from the largely more generalized lizard type, and always consists of only one bar, simple or recurved, on each side. These bars are joined anteriorly in most species, and in these species there may or may not be a prominent lingual process. (See Figs. 1 and 2.)

The hyoid's position is rather constant: on the under surface of the head and neck, immediately deep to the muscles beneath the skin in this area. However, in the anomalepidids, typhlopids, and leptotyphlopids, the hyoid lies completely posterior to the head. It can generally be said that except in those families just mentioned the anterior end of the hyoid closely approximates the position of the first ventral scute. There is a reason for this: the anterior fibers of the *costocutaneus superior* muscle originate on the anterior fraction of the hyoid and insert on the few first scutes.

In colubrids and all families of poisonous snakes, the anterior part of the hyoid lies deep to the *costocutaneus superior*, and the posterior part of the hyoid lies deep to the *obliquus internus* plus *transversus abdominis*.

In boids, xenopeltids, aniliids, and uropeltids, the hyoid lies deep to

the *costocutaneus superior*, but peripheral to the *obliquus internus* plus *transversus abdominis*.

In the genus *Cylindrophis* (Aniliidae), the hyoid cornua are very reduced and the *costocutaneus superior* muscle has no connection with them. This is also true for uropeltids.

The typhlopids and leptotyphlopids are unique in having the hyoid buried in the extrinsic tongue muscles, which, in turn, lie deep to the *obliquus internus* plus *transversus abdominis*.

B. Form and Composition

The hyoid apparatus in snakes is derived from branchial (pharyngeal, visceral) arch cartilages, as in other vertebrates. Branchial arches are here taken to mean the entire arch series, including the jaw arches. The exact contributions of the several arches to the hyoid in snakes are, frankly, not altogether clear; this subject will be discussed later in this section.

As a preliminary step, it seems wise to review the hyoid of lizards, where the structure is much easier to deal with than in snakes.

Lizard Hyoids. The hyoid varies in form and obviously in derivation among lizards, but the sources of the parts seem fairly straightforward. In general, three branchial arches — 2, 3, and 4 — contribute cartilages to the lizard hyoid, but many lizard species have hyoids derived from only two arches.

In the most complete type, which is also common to adult amphibia, and may be considered as the basic generalized lizard type, all three arches contribute (Fig. 1, B). The development of this generalized type can be followed quite easily in early embryonic stages. Kallius (1901) and El-Toubi and Kamal (1959) have shown and illustrated this very well. Derivatives of the three arches are identifiable in this way: 2nd arches — lingual process (processus entoglossus), basihyal (body of hyoid), paired hypohyals and ceratohyals; 3rd arches — paired 1st ceratobranchials; 4th arches — paired 2nd ceratobranchials. The three paired cartilages form the three pairs of cornua, or bars, on each side.

Of the 2nd arch parts, the lingual process and basihyal are median in position, although the basihyal is probably often forked posteriorly. The hypohyals fuse with the basihyal and routinely are directed anteriorly to some degree; the ceratohyals are generally direct continuations of the hypohyals but are always at an angle with the hypohyals, being directed posteriorly. In some species the hypohyals are actually physically separated from the ceratohyals. In many species the cerato-

hyals have recurrent cornua directed anteriorly which often reach the stapes. The 2nd arch parts are always cartilaginous in lizards.

Of the 3rd arch parts, the 1st ceratobranchials are usually sturdy in form and commonly bony, entirely or in part. The cornua are typically slightly bowed or curved, divergent from midline, and are directed posteriorly. The 1st ceratobranchial cornua usually articulate with the basihyal by a distinct joint, which at least in some cases appears to be discontinuous. The hyoglossal muscles always attach to the 1st ceratobranchials.

Of the 4th arch parts, the 2nd ceratobranchials are always cartilaginous and are usually very long. These cornua are parallel to the midline and often close together, sometimes touching for their entire length. They are fused to the basihyal.

It is not known whether hypobranchial elements, derived from the 3rd and 4th arches, contribute to the basihyal median piece in lizards.

Many species of agamids, gekkonids, iguanids, lacertids, and scincids have the complete generalized type. Few other families have species which do.

Most lizards have a hyoid in which the 2nd ceratobranchials are lacking, so that the structure consists of the lingual process, basihyal, and two pairs of cornua — hypohyals plus ceratohyals and the 1st ceratobranchials. Examples are: *Varanus* (Fig. 1, A), *Gerrhonotus* (Fig. 1, D), *Gehyra* (Fig. 1, E), *Xenosaurus* (Fig. 1, G), *Lanthanotus* (Fig. 2, B), *Anguis* (Fig. 2, C), *Heloderma* (Fig. 2, D), and *Rhineura* (Fig. 2, E). In some genera, e.g., *Lanthanotus*, *Anguis*, and *Rhineura*, the 2nd arch cornua are reduced to anteriorly directed rods which probably are the hypohyals alone; if so, then, of course, the ceratohyals are missing.

The genus *Anniella* is the only lizard genus in which the author has found by dissection a hyoid composed of a single pair of cornua plus the lingual process and basihyal (Fig. 2, A). These cornua are considered 1st ceratobranchials because they are bony, diverge in a posterior direction from the midline, and are the attachments for the hyoglossal muscles; in general form they also closely resemble the 1st ceratobranchials in hyoids of the complete generalized type. Versluys (1936) stated that "*Dibanus*" (should be *Dibamus*) is like *Anniella* and has a reduced hyoid with only one pair of cornua — the 1st ceratobranchials.

It seems that in lizards retention of either the 2nd arch cornua or the 4th arch cornua alone is never found. The lingual process is found in all lizards, as far as is known.

Lizard hyoids are generally well developed, relatively large, and, as just indicated, commonly with at least two pairs of cornua in some

form. However, in burrowing lizards, particularly, the hyoid tends to be reduced in relative size; e.g., *Amphisbaena* (Fig. 1, C), *Anguis*, *Rhineura*, and *Anniella*. In the first three genera, the 2nd and 3rd arch cornua are present. The special case of *Anniella* has already been given.

Among anguinomorphan lizards, which are perhaps the ancestral group for snakes, probably a majority of the modern species have the most common lizard type — composed of parts from the 2nd and 3rd arches, and having two pairs of cornua. Examples are: *Varanus* (Fig. 1, A) *Gerrhonotus* (Fig. 1, D), and *Xenosaurus* (Fig. 1, G).

Snake Hyoids. The hyoids of snakes are more of a problem to understand than those of lizards because identities of the cornua are not at all certain. This is because snake hyoids are severely reduced in composition, and it is true that in matters of evolution where parts have been lost, identity of what remains is apt to be very difficult to establish.

Snake hyoids are cartilaginous with the exception of the genus *Typhlops*, where the hyoid is entirely or partly bony in some specimens. In a specimen of *T. schlegeli mucruso*, for example, the entire hyoid was bony, but in a specimen each of *T. schlegeli brevis*, *T. polygrammicus*, and *T. bibroni*, it was cartilaginous. Age may be the important factor here. Anyway, only in typhlopids does the hyoid become bony. Hyoids of many presumably old specimens of various species of snakes are often found to be calcified, that is, quite hard and brittle. List (1966) mentioned that he found calcification in the hyoids of many leptotyphlopids.

There are four morphological groups of snake hyoids (Fig. 1, H, J-M). These groups are remarkably constant, and are noticeably distinct from each other. The families of snakes can be fit very neatly into these morphological groups, with only several genera as exceptions.

The four groups are simply called: (1) "M" type, (2) "Y" type, (3) "V" type, and (4) parallel type.

(1) "M" type (Fig. 1, H). This type is found exclusively in the Anomalepididae, a neotropical family of four fossorial, closely allied genera: *Anomalepis*, *Liotyphlops*, *Helminthophis*, and *Typhlophis*. The first three genera have been examined for the hyoid, and it has been found to be similar in all specimens. The apparatus is basically M-shaped, with the posteriorly directed cornua having recurrent parts as long or longer than the cornua themselves.

The transverse cartilage is depressed centrally to show a concave surface anteriorly. The transverse piece then curves posteriorly on each side, and is directed posteriorly and a little laterally. The re-

current cornua are very thin and also tend to curve somewhat medially; in some specimens these recurrent cornua can be traced to the skull. It should be noted that in this type the hyoid is a cartilaginous, slender, continuous strand with no visible joints.

The described parts can be identified as follows: the central concave part is provisionally called the basihyal; the adjacent convex parts of the cornua are called the hypohyals; the posteriorly directed cornua are the ceratohyals; the recurrent cornua are merely recurrent parts of the ceratohyals. The hyoglossal muscles attach only to the ceratohyals because these are the only parts of the hyoid available for attachment. Therefore, in anomalepidids the hyoid is considered by the author to be composed entirely of contributions from the 2nd branchial arches.

No lingual process is present.

Identification of the parts is based on direct comparison with lizard hyoids. For example, in Fig. 1, item G is the hyoid of the lizard *Xenosaurus grandis*, and H is that of *Liotyphlops*, an anomalepidid. Note the striking similarity of the 2nd arch cornua of *Xenosaurus*, or of nearly any other lizard for that matter, to the anomalepidid hyoid. In short, if the lingual process and the 1st ceratobranchials were removed from the hyoid of *Xenosaurus*, the remaining parts would appear very much like the anomalepidid hyoid. Actually, whether or not the medial concave segment represents the basihyal is problematical.

Smith and Warner (1948) made the same identities. List (1966) has taken a similar stand. McDowell and Bogert (1954) assumed that the hypohyals meet in a median symphysis; this could just as well be true as not. McDowell and Bogert also were of the opinion that the anterior element discovered by Dunn and Tihen (1944) lying between the lower jaws in *Liotyphlops* represented part of the glossal skeleton. It is true that this element in stained specimens does resemble an inverted "Y" hyoid as seen in *Typhlops*, but Warner (1948) conclusively showed this to be the ventral cricoid arch of the larynx, and simultaneously showed that what Dunn and Tihen finally decided to be a pectoral girdle was nothing more or less than the hyoid. Gross dissection easily substantiates Warner's stand (Fig. 7). In this figure the cricoid arch of the larynx is hidden from view by the tongue, but the hyoid and its muscles are shown.

The fact that the recurrent cornua extend forward to the skull in at least some specimens, as reported by Smith and Warner, is surely more evidence for a 2nd arch derivation, since the 2nd arch hyoid derivatives in vertebrates commonly retain such a connection.

(2) "Y" type (Fig. 1, J, K). The Typhlopidae and Leptotyphlopidae,

each family with a single recognized genus, have this hyoid type. Basically it is similar in appearance to an inverted Y, with the single, long, median lingual process directed anteriorly, and the two cornua directed posteriorly and somewhat divergent from the midline.

List (1966), however, in his examination of the osteology of these animals, showed by clearing and staining that a specimen each of *T. lumbricalis* and *T. pusillus* did not have the lingual process, so that the hyoid was reduced to a pair of subparallel cornua (Fig. 2, G). The author has checked a second specimen of each species: the lingual process was lacking in *T. pusillus*; in *T. lumbricalis* there was a very small process which was joined to the two cornua. List also found that in several other species of *Typhlops* that he examined the cornua were not fused with the lingual process — there being a distinct gap between the median piece and each cornu (Fig. 2, F); *T. reticulatus*, *T. platycephalus*, and *T. blanfordi lestradei* showed this condition. The author has dissected a second specimen of *T. reticulatus* and found that no lingual process was evident, so that the two cornua were separated anteriorly. None of the other species of *Typhlops* examined by the author either lacked a process or had the cornua separated from the lingual process.

The species of *Leptotyphlops*, as far as known, invariably retain the complete Y form.

Identification of the parts is as follows: the median piece is certainly the lingual process, which incorporates the basihyal; the cornua are considered to be the 1st ceratobranchials. The hyoid may be totally bony in many typhlopoid specimens, or else the cornua alone may be bony (Fig. 2, F and G). The hyoglossal muscle fibers attach individually to the cornua.

The identification is based upon comparison with lizard hyoids. In *Anniella* the hyoid consists of a lingual process plus basihyal and one pair of cornua, the 1st ceratobranchials, which are bony and to which the hyoglossal muscles attach as in all other lizards. The "Y" type snake hyoid bears a great resemblance to that of *Anniella* or to that of any lizard with the basihyal and 1st ceratobranchials taken alone; the cornua are frequently bony in typhlopids, and they also provide attachment for the *hyoglossi*.

List (1966) felt that there seemed to be three conditions present in the typhlopids: (1) basihyal and lingual process with 1st ceratobranchials; (2) lack of basihyal and lingual process, leaving only the two 1st ceratobranchials; (3) basihyal and process only, with loss of ceratobranchials. He indicated that a series can be arranged to show the regressive change from the basic condition (1) to conditions

(2) and (3). This series seems reasonable, but condition (3) cannot be conclusively proven without embryological evidence. List showed several *Typhlops* with an obvious basihyal cartilage separated from the bony 1st ceratobranchials: *T. reticulatus* (Fig. 2, F), and *T. blanfordi lestradei*. He illustrated condition (2), with the basihyal lacking and only 1st ceratobranchials present, in *T. pusillus* (confirmed by the author) and *T. lumbricalis* (a small process in a second specimen). He figured several more species which he interpreted as having only the basihyal present as condition (3): *T. braminus*, *T. polygrammicus* (Fig. 2, H), and *T. vermicularis*; this basihyal element always proved to be cartilaginous, with the prongs relatively short. The author has checked a second specimen of *T. polygrammicus* and the hyoid is also cartilaginous.

As mentioned, ossification in the hyoid of typhlopids is variable. A large specimen of *T. schlegeli mucruso* was found to have a completely ossified hyoid. List found the same condition in a specimen each of *T. boettgeri* and *T. s. schlegeli*. However, the author found the hyoid to be totally cartilaginous in a specimen of *T. schlegeli brevis*. Very possibly the matter of ossification may be directly correlated with age.

Smith and Warner (1948) supposed that the hyoid of the "Y" type is composed of a median basihyal and its process plus the cornua, which are implied in previous paragraphs of their paper to be equal to the hypohyals. Comparison with most lizard hyoids easily shows this idea to be of little value, for in lizards the hypohyals lie in a transverse or anterolateral plane and are never bony.

For the species of examined leptotyphlopids, the hyoid is very constant: it is always cartilaginous, the lingual process is joined to the cornua, and the cornua are usually relatively longer than in *Typhlops* (Fig. 2, J).

The relationship of the typhlopid and leptotyphlopid snakes is not clear, and the two families have often been considered by some workers, e.g., McDowell and Bogert (1954), to be very distantly related, if at all in any sort of recent sense. However, the hyoid, which is similar for the two families and yet is distinct from all other snakes, tends to indicate that these families have more of a relationship than might otherwise be awarded them. This viewpoint is materially strengthened by musculature patterns presented in the second part of this paper. McDowell and Bogert combined typhlopids and the anomalepidids into the Typhlopidae. They felt that "the hyoid of *Typhlops* differs from that of ordinary snakes, leptotyphlopids, and the vast majority of lizards" in having the hyoid confined to the tongue itself. Actually,

Leptotyphlops has nearly the same muscle-hyoid relationships that are found in *Typhlops*. They also regarded the hyoid of *Typhlops* as being composed of the basihyal alone. Then they proposed that the leptotyphlopids and other snakes' hyoids are composed of a fused basihyal plus 1st ceratobranchials, except where the basihyal has been secondarily lost. The opinion of List on the possibility that the basihyal alone may compose the hyoid in at least some typhlopids has been given previously; the author does not disagree with it. However, the author cannot agree that *Leptotyphlops* and "ordinary snakes" all have the same components forming the hyoid; even so, McDowell and Bogert did devise the correct combination of basihyal and 1st ceratobranchials for the leptotyphlopids.

(3) "V" type (Fig. 1, L). This is found in the families Aniliidae, Boidae (with the exception of several puzzling genera), Uropeltidae, and Xenopeltidae. The hyoid is basically of an inverted V form, or is reduced, by loss of the anterior connection and parts of the cornua, to a pair of subparallel rods. The cornua diverge posteriorly from the midline and may be slightly bowed. They are always cartilaginous and the hyoglossal muscles attach to them as separate bundles. No lingual process is present and the arch of the cornual union is very slender when present.

Loss of the anterior connection may not perhaps have much meaning phylogenetically; for example, in one specimen of *Charina bottae*, the cornua were joined anteriorly, but in another, they were not. A specimen of *Epicrates angulifer* had the cornua united, but a specimen of *E. cenchris* did not.

It seems evident to the author that the cornua of this type must be 1st ceratobranchials, and that the basihyal is either very small in those hyoids that have united cornua, or else entirely absent, which it certainly is in the many cases where the cornua are distinctly separated anteriorly. Again it is comparison with lizards that gives the answer. The cornua of the "V" type are definitely very similar in general appearance and position to the 1st ceratobranchials in lizards. Remove the entire basihyal, hypohyals, ceratohyals, and 2nd ceratobranchials from a generalized lizard hyoid, such as *Anolis* (Fig. 1, B), or the entire basihyal, hypohyals, and ceratohyals from the more common lizard type, as seen in *Varanus* (Fig. 1, A), *Gerrhonotus* (Fig. 1, D), or *Gehyra* (Fig. 1, E), and the 1st ceratobranchial cornua that are left certainly resemble the cornua of the "V" type.

The author considers the basihyal to be missing, for all practical purposes, but Edgeworth (1935) stated, with no further discussion, that *Boa* and *Python molurus* have the anterior ends of the cornua

"continuous with a small basihyobranchiale." To the contrary, Gnanamuthu (1937) from Fürbringer stated that in *Python* the "basi-hyoid" is gone and the two "thyrohyals" (meaning the cornua) are practically free of each other. "Thyrohyal" is a name reserved for an element from the 3rd branchial arch. It is not customarily used in lizards, and it seems improper to sanction the use of the word in snakes. Smith and Warner (1948) have stated a similar view, but proposed at the same time to call the cornua of the "V" type the hypohyals. From comparison with lizards, it does not seem likely that these could be equal to the hypohyals.

(4) Parallel type (Fig. 1, M). This type is found in colubrids, hydrophids, elapids, viperids, and crotalids, and in a few genera of what are usually considered to be boids: *Bolyeria*, *Casarea*, *Trachyboa*, and *Tropidophis*. The parallel type consists of a pair of very long parallel cornua which are always joined anteriorly. The arch of this union is sometimes smooth and sometimes has an anteriorly directed lingual process. This hyoid type is always cartilaginous. The cornua provide the attachment for the hyoglossal muscles.

Identification of the parts is as follows: the lingual process, if present, is obvious; the arch at the union of the cornua is considered to be the basihyal, although it perhaps is not really present when there is no lingual process; the cornua are considered to be the 2nd ceratobranchials. The cornua are always fused indistinguishably with the basihyal arch, or at least to each other.

The little work that has been done on the development of the snake hyoid has all centered on the parallel type. This evidence has not been satisfactory overall; it has been conflicting in part and the early blastemal stages of the hyoid components have not been identified. It can be pointed out that this problem, as well as a great many others in the subject of snake ontogeny, presents a worthwhile and fertile field for investigators. The author has studied fairly early embryos of both *Pituophis* and *Thamnophis* but has not yet been satisfied as to the origin of the parts of the parallel type hyoid. The embryological evidence must at this time largely yield to the morphological comparison with lizard hyoids.

There has been no trouble with the identification of the basihyal and its lingual process, if one is present. They are certainly 2nd arch derivatives. It is the cornua which have given identity problems. Most investigators have called the cornua ceratohyals, or at least have meant that they are of 2nd arch derivation. A lesser number of investigators have considered the cornua to be 1st ceratobranchials, of 3rd arch derivation. And, as already noted above, the author

considers the cornua to be the 2nd ceratobranchials, of 4th arch derivation.

Rathke (1839) claimed to have observed a connection between the cornua and the columella auris in *Tropidonotus*; this observation was offered to substantiate his view that the cornua are 2nd arch derivatives.

Owen (1866) called the cornua ceratohyals, as did Walter (1887). McKay (1889) varied the name somewhat by calling the cornua "hyoid bones" or "hypobranchial bars." Neither term is very appropriate. Gaupp (1904) followed Rathke in deciding that the cornua are 2nd arch derivatives and called them "cornua hyalia."

Peyer (1912) studied several stages of *Vipera aspis*. He could not find a 3rd branchial arch in his embryos, and also did not observe a connection between a cornu and the columella auris, as Rathke claimed to have seen. At the 70-mm stage, Peyer said that the hyoid consisted of two "hyal cornua" with a separate, anterior "processus entoglossus." In the 125-mm stage, the hyoid was complete. The cornua were definitely shown to originate in a nearly parallel fashion posterior to the basihyal element — the lingual process; the cornua then grew anteriorly to meet the process.

Sewertzoff (1929) called the cornua the ceratohyals. Bäckström (1931) did not positively name the cornua but implied that they are of 2nd arch derivation.

In 1935 Edgeworth called the single element of the hyoid the "basihyobranchiale" and the cornua the "cornua branchiale i." He also stated that he believed the ceratohyals have been lost. No reasons were given for any of his conclusions, however.

Versluys (1936) called the connecting piece the "corpus hyale" but used Fürbringer's (1922) interpretation in naming each cornu the "cornu branchiale I." Versluys based his conclusion on the comparison with the reduced hyoids of the lizards *Anniella* and *Dibamus*, where it is probable that the cornua are the 1st ceratobranchials. DeBeer (1937) called the cornua the ceratohyals.

Kesteven (1944), from observations on *Pseudechis*, an elapid, remarked that "this single hyoid arch is probably the second; it appears too far back to be the ceratohyal." Apparently Kesteven called the 2nd arch of the series the 1st branchial arch, a common procedure in comparative anatomy (the 1st arch of the series — mandibular plus maxillary processes — would compose the jaw arch). If such is the case, then the "second" arch he referred to would be the 3rd branchial arch of this paper. Kesteven therefore considered the hyoid cornua to be the 1st ceratobranchials.

Smith and Warner (1948) used basihyoid plus hypohyals for the components. It does not seem to the author that hypohyals are a reasonable choice. In lizards they are always in a transverse or anterior-directed plane and relatively short.

Cowan and Hick (1951) used ceratohyals for the cornua in *Thamnophis*. These authors found two tendinous inscriptions in the *neurocostomandibularis* muscle of *Thamnophis*, and they considered these inscriptions to be traces of the 1st and 2nd ceratobranchials. However, the possibility of the inscriptions being traces of the 1st and 2nd ceratobranchials would not correctly fit with their interpretation of the cornua as ceratohyals, because the ceratohyals would be in the wrong position relative to the ceratobranchials. If anything, their suggestion as to the identity of the inscriptions would fit in better with the author's idea that the cornua are 2nd ceratobranchials.

In 1954 McDowell and Bogert stated that the parallel type of snake hyoid consists of a basihyal fused to the 1st ceratobranchials. They arrived at this solution by comparing the hyoids with those of lizards, but the drawback is that they included *Leptotyphlops* with the group represented by the parallel type. It is surely clear that *Leptotyphlops* has a hyoid which is distinctly different from the parallel type, and is really similar to that of *Typhlops*. The author does consider the "Y" type of hyoid as seen in the leptotyphids and typhlophids as being basically composed of a basihyal plus 1st ceratobranchials.

Pringle (1954) has done considerable work on the cranial development in snakes, studying the colubrids *Lamprophis ornatus* and *Dasypeltis scaber*, the viperid *Causus rhombeatus*, and the elapid *Hemachatus hemachatus*. He named the cornua the ceratohyals.

In the 69-day stage of *Lamprophis*, he noted that the "two ceratohyals fuse below; basihyal present." He also noted that during development the basihyal moves forward.

In the 43-day stage of *Dasypeltis*, "the hyobranchial apparatus consists of two ceratohyals which fuse anteriorly." He found no basihyal at this stage; later, however, the basihyal appeared.

As for the 54-day stage in *Causus*, the "ceratohyals" fused below the basicranial fenestra. He saw no basihyal in this species, even in the young adult.

In *Hemachatus* the 8-mm stage revealed that the "ceratohyals fuse below the basicranial fenestra, and during development this point of fusion moves forward. There is no basihyal in any of the stages examined as in *Causus*."

It is evident that at least in these genera the cornua fuse first, and the basihyal element, if there is one, later fuses to this union. A

check of specimens by the author revealed that both *Causus* and *Hemachatus* lack a lingual process in the adult, as suggested by Pringle; this seems to indicate that a rounded arch means absence of all basihyal elements.

There were no particular reasons advanced by Pringle for calling the cornua ceratohyals. And it might easily be construed that the matter of the fusion of the cornua and their subsequent moving forward would be evidence for their being derived from an arch other than the 2nd. The later fusion of the obvious basihyal piece, where it was present, would add support to this idea.

Srinivasachar (1954) called the cornua ceratohyals; he gave no reasons.

List (1966) decided that since the basihyal may be the only piece present in some typhlopids and is the only piece present in *Leptotyphlops*, it must also compose the entire hyoid in those snakes with the parallel type. The long cornua, according to him, would merely represent elongations of the posterior basihyal processes. In his interpretation the processes would not strictly be hypohyals or ceratohyals, apparently. List's idea is not an unattractive one, but there are arguments against it. One is that *Typhlops* must be far removed phyletically from the snakes with a parallel hyoid, so what is true for the typhlopids and leptotyphlopids would not necessarily apply to the parallel type. A second argument is that Pringle has shown in several species that the cornua develop separately from the basihyal element, if one is present at all.

Romer (1956) stated that "the 'prongs' are presumably the first branchials; the small connecting piece, the corpus, with a short lingual process."

Sondhi (1958) called the basihyal the basihyoid, and used only cornua for those bars. He also parenthetically referred to Versluys by including the latter's respective synonyms: corpus hyale and cornua branchialia I. Apparently he followed Versluys in believing the cornua to be 1st ceratobranchials.

Albright and Nelson (1959) considered that the hyoid in *Elaphe* is composed of a "basihyoid with paired ceratohyals." They gave no explanation for their choice.

In 1961 El-Toubi and Magid considered that the cornua are derived from the 2nd arch. The most recent paper, and probably the best, to appear on the development of the snake skull is the one by Kamal and Hammouda (1965) who studied very closely the ontogeny of the skull of *Psammophis sibilans*, a colubrid. This paper is especially interesting because it clearly seems to refute some of the evidence

of Pringle, but also seems to substantiate List's idea that the cornua are extensions of the basihyal.

In their "stage I, age 15 days, 47 mm" of *Psammophis* embryos, Kamal and Hammouda found, and clearly illustrated, a small inverted v-shaped body which was chondrifying and lay between Meckel's cartilages. At stage II the piece had a distinct anterior projection on it which the authors called the processus entoglossus. At stage III both the process and the posterior-directed prongs had enlarged and lengthened so that the piece was rather y-shaped. At stage IV the prongs had lengthened noticeably and were called the ceratohyals. Successive stages clearly demonstrated that the ceratohyals were formed by the increase in length of the two rods. Kamal and Hammouda have shown very well that in *Psammophis* the cornua have grown from a common piece and have not formed independently of the basihyal element as Pringle demonstrated. However, have they really proved, as List thought, that the parallel type cornua are extensions of the basihyal? List's conclusion appears very convincing at first glance, but the heart of the matter is understanding from what the chondrifying blastema has been derived. Kamal and Hammouda, for all their very good work, have not really demonstrated whether the initial v-shaped piece has been derived of blastemal material from the 2nd arches alone, or whether blastemal material from another set of arches, particularly the 4th, has also contributed. Blastemal origin, then, is the crux of the problem, and until this is solved, the exact explanation of the derivation of the parallel type of hyoid's cornua must be based on morphological evidence.

At the conclusion of this review of the literature on the problem, it might as well be mentioned that many authors have just regarded the apparatus as the "hyoid" and let it go at that. A short summary of the pertinent nomenclature of the parts of the parallel type hyoid should prove helpful.

- 1839 Rathke: cornua hyalia (2nd arch)
- 1866 Owen: ceratohyals
- 1887 Walter: ceratohyals
- 1889 McKay: hyoid bones or hypobranchial bars
- 1904 Gaupp: cornua hyalia (2nd arch)
- 1912 Peyer: hyal cornua with processus entoglossus
- 1929 Sewertzoff: ceratohyals
- 1931 Bäckström: 2nd arch origin inferred
- 1935 Edgeworth: basihyobranchiale plus cornua branchialia i
- 1936 Versluys: corpus hyale plus cornua branchialia I
- 1937 DeBeer: ceratohyals
- 1944 Kesteven: not named directly, but apparently 1st ceratobranchials
- 1948 Smith and Warner: basihyoid plus hypohyals

- 1951 Cowan and Hick: ceratohyals
- 1954 McDowell and Bogert: basihyal plus 1st ceratobranchials
- 1954 Pringle: basihyal plus ceratohyals
- 1954 Srinivasachar: ceratohyals
- 1956 Romer: corpus, lingual process, and "presumably the first branchials"
- 1958 Sondhi: basihyoid plus posterior cornua
- 1959 Albright and Nelson: basihyal plus ceratohyals
- 1961 El-Toubi and Magid: derived from 2nd arch
- 1965 Kamal and Hammouda: processus entoglossus plus ceratohyals
- 1966 List: basihyal plus basihyal processes

The history shows that most investigators have regarded the cornua as ceratohyals; few have shown any reasons for their actions. Only Rathke, Peyer, Pringle, and Kamal and Hammouda have used embryological evidence, and this seems to be somewhat contradictory in a few respects. The author's conclusion that the cornua are 2nd ceratobranchials is only based upon direct comparison with the complete generalized lizard hyoid type. A look at one of these generalized lizard hyoids, e.g., *Anolis* (Fig. 1, B), will demonstrate what is meant: by removing the hypohyals plus ceratohyals and the 1st ceratobranchials, the remaining continuous cartilage will be composed of the lingual process, a basihyal arch, and the very long, parallel cornua, the 2nd ceratobranchials. The similarity of this altered hyoid of *Anolis* to that of any snake with a parallel type hyoid (including a lingual process) is remarkable. It is true that in the lizard, the *hyoglossi* attach to the 1st ceratobranchials. However, if only the 2nd ceratobranchials are present in certain snakes, these are obviously the only cornua which are available for the *hyoglossi*. Note that in the lizards *Amphisbaena* (Fig. 1, C) and *Mabouia* (Fig. 1, F), the hyoids as a whole are somewhat reduced, and the 2nd ceratobranchials in particular are relatively very short. In these species the 2nd ceratobranchials resemble very much the developing cornua of the parallel type hyoid as shown by Kamal and Hammouda.

C. Descriptions of Examined Hyoids

The following measurements are given in millimeters (mm). Those measurements concerning the hyoid are rounded to the nearest .5 mm. Due to the natural difficulty of measuring cartilaginous strands in preserved specimens, the results have to be regarded chiefly as a means of comparing relative sizes of various hyoids.

In the parallel type of hyoid, the width of the hyoid is that measurement taken at the greatest width of the two cornua. Actually, the arch of the basihyal is usually somewhat more narrow than the width. The

length of the parallel type of hyoid is its entire length — from the tip of the lingual process, if one is present, to the end of the cornua.

Museum abbreviations are: UI, University of Illinois Museum of Natural History; CNHM, Chicago Natural History Museum; USNM, United States National Museum; MCZ, Museum of Comparative Zoology, Harvard University.

ANOMALEPIDIDAE ("M" type)

Helminthophis flavoterminalis (USNM 69333). Hyoid not measured but with same essential shape and relationships as in the following species.

Liotyphlops albirostris (MCZ 25232) (Fig. 1, H). Recurrent continuations extend craniad from the legs of the "M"; central depression 4 mm from mental; width of shoulders of transverse bar 1 mm; length of one descending cornu 2 mm; length of one ascending (recurrent) cornu 1.5 mm. Body length 181 mm.

TYPHLOPIDAE ("Y" type)

Typhlops bibroni (CNHM 17718) (Fig. 8, B). Hyoid cartilaginous; process 1.5 mm, 20 mm from mental; one cornu 2 mm; posterior separation of cornua 2 mm; hyoid lies between ribs 9-11. Body length 375 mm.

Typhlops intermedius (CNHM 53636). Hyoid cartilaginous; process 1.5 mm, 24 mm behind mental; hyoid median length 2 mm; hyoid lies between ribs 11-13. Body length 313 mm.

Typhlops schlegeli mucruso (CNHM 81018) (Fig. 1, J). Hyoid bony; process 1.5 mm, 33 mm behind mental; hyoid median length 2.5 mm; posterior separation of cornua 1.5 mm. Body length 365 mm.

LEPTOTYPHLOPIDAE ("Y" type)

Leptotyphlops maximus (CNHM 38282) (Fig. 1, K). Process 2 mm, 16 mm behind mental at 9th rib; hyoid median length 6 mm. Body length 326 mm.

Leptotyphlops septemstriatus (CNHM 26660). Process 1.5 mm, 12 mm behind mental; one cornu 2.5 mm; hyoid lies between ribs 6-13. Body length 245 mm.

UROPELTIDAE ("V" type)

Platyplectrurus madurensis (CNHM 40458). Cornua separated

anteriorly by 3 mm, posteriorly by 6 mm; median length 7.5 mm; hyoid ends 5th ventral. Body length 285 mm.

Rhinophis blythi. Three specimens examined, all with cornua separated anteriorly; measurements of two specimens given. In CNHM 25930 (Fig. 11), cornua separated anteriorly by 2 mm, posteriorly by 4 mm; cornua 7.5 mm behind mental; median length of hyoid 3.5 mm; cornua begin 1st ventral, end 4th. Body length 282 mm.

In another specimen, cornua separated anteriorly by 2 mm, posteriorly by 7.5 mm; cornua 6 mm behind glottis; cornua 5.5 mm, begin 1st ventral, end 6th. Body length 255 mm.

Rhinophis planiceps. Cornua separated 1.5 mm anteriorly, 3 mm posteriorly; cornua 4.5 mm behind glottis; cornua 2.5 mm, begin 1 mm anterior to 1st ventral, end rear of 2nd; cornua nearly parallel for first quarter, then flare laterally. Body length 167 mm.

Silybura beddomii (CNHM 16110). Cornua separated anteriorly by 2 mm, posteriorly by 4 mm; cornua 6.5 mm behind mental; hyoid median length 3.5 mm. Body length 159 mm.

ANILIIDAE ("V" type)

Anilius scytale. Four specimens examined, all with cornua joined anteriorly and with no process; measurements of two specimens are given. In CNHM 16943 point of arch 8.5 mm anterior to 1st ventral; cornua end 2nd ventral; arch .5 mm wide; right cornu 10 mm, left cornu 12 mm; cornua separated anteriorly by 7 mm; anterior parts of cornua very thin. Body length 537 mm.

In CNHM 35683 (Fig. 12, A), point of arch 20 mm from mental; cornua separated posteriorly by 8 mm; hyoid median length 15 mm. Body length 770 mm.

Cylindrophis maculatus. Hyoid much reduced. In MCZ 15795 (Fig. 12, C), cornua 14.5 mm behind mental, separated anteriorly by 6 mm. Cornua 4 mm, begin 3 mm behind hyoglossal split; anterior half of each cornu free from hyoglossal muscle. Body length 315 mm.

In CNHM 25928, cornua 12 mm behind mental; cornua separated anteriorly by 2.5 mm, posteriorly by 4 mm; cornua end 7th ventral; hyoid median length 2 mm. Body length 283 mm.

Cylindrophis rufus. Two specimens examined have separate cornua. In CNHM 67269 (Fig. 12, B), cornua 15.5 mm behind mental; cornua separated anteriorly by 2.5 mm; cornua begin 4th scale anterior to 1st ventral, end 3rd ventral; hyoid median length 8.5 mm. Body length 490 mm.

In CNHM 30547, cornua 11.5 mm behind mental; cornua separated

anteriorly by 3 mm; posteriorly by 7.5 mm; hyoid median length 4.5 mm. Body length 401 mm.

XENOPELTIDAE ("V" type)

Xenopeltis unicolor. Three specimens examined, all have divergent cornua joined anteriorly. In CNHM 15273 (Fig. 13), point of arch 14 mm behind glottis; hyoid begins 5 mm before 1st ventral, ends 9th ventral; cornua 30 mm, separated posteriorly by 12 mm. Body length 698 mm.

In another, unnumbered specimen, arch 23 mm behind mental; arch 1 mm wide; hyoid begins 1st ventral, ends 11th; cornua separated posteriorly by 10 mm; hyoid median length 26 mm. Body length 770 mm.

BOIDAE (*sensu lato*) ("V" type and parallel type)

Aspidites melanocephalus (USNM 11034). Cornua joined anteriorly as rounded arch; hyoid begins 20 mm before 1st ventral, ends 6th ventral; cornua separated posteriorly by 19 mm; cornua 35 mm. Body length 987 mm.

Boa canina (CNHM 25537). Cornua separated anteriorly upon dissection, but may have been joined naturally; cornua begin 12 mm behind glottis, end 4th ventral; cornua 13.5 mm. Body length 610 mm.

Boa cookii (CNHM 41171). Cornua separated anteriorly; cornua begin 17 mm behind glottis, end 4th ventral; hyoid median length 18 mm. Body length 1380 mm.

Calabaria reinhardtii (USNM 24224). Cornua joined anteriorly by a very thin arch; arch 6 mm behind glottis; arch 1.5 mm wide; cornua separated anteriorly by 10.5 mm; cornua 21 mm and 20.5 mm long. Body length 563 mm.

Charina bottae. In three specimens examined, cornua are close anteriorly but do not join in two; cornua joined as a rounded arch in the third. In one of the former specimens, cornua separated anteriorly by .5 mm, posteriorly by 14 mm; cornua end at rear edge of 2nd ventral; cornua 15.5 mm. Body length 494 mm.

In the specimen with cornua joined, arch lies 8.5 mm anterior to 1st ventral; hyoid ends 3rd ventral; arch 2.5 mm wide; cornua separated posteriorly by 8 mm; hyoid median length 11 mm. Body length 411 mm.

Chondropython viridis (CNHM 14075). Cornua rather flat and joined anteriorly; arch 20 mm behind mental; cornua end 5th ventral;

cornua separated posteriorly by 6 mm; hyoid length 24.5 mm. Body length 930 mm.

Constrictor constrictor ortonii (CNHM 8360). Cornua separated anteriorly, begin 16 mm behind glottis, end just anterior to 1st ventral; cornua separated anteriorly by 3 mm, posteriorly by 15.5 mm; hyoid median length 16 mm. Body length 1000 mm.

Enygrus bibronii (USNM 56211). Cornua joined at a narrow, sharp-pointed arch 9 mm behind glottis; cornua 12 mm, end at rear edge of 2nd ventral; cornua separated posteriorly by 8.5 mm. Body length 505 mm.

Epicrates angulifer (USNM 84045). A blunt arch 8.5 mm behind glottis; arch 6 mm wide; cornua 17.5 mm, separated posteriorly by 8 mm. Body length 592 mm.

Epicrates cenchris (CNHM 31143) (Fig. 14, C). Cornua separate, begin 20 mm behind mental, end 5th ventral; cornua separated anteriorly by 1.5 mm; cornua 23 mm. Specimen is head only.

Eryx c. colubrinus (CNHM 81224) (Fig. 14, B). Cornua joined anteriorly into irregular arch 12 mm behind mental; arch 2 mm wide; cornua separated posteriorly by 11 mm; hyoid length 18 mm. Body length 590 mm.

Eryx jaculus. In two specimens examined cornua are separate; one set of measurements given. In USNM 56348, cornua begin 10 mm behind glottis; cornua separated anteriorly by 3.5 mm, posteriorly by 12 mm; right cornu 13 mm, left cornu 16 mm. Body length 487 mm.

Eryx johnei (USNM 84034). Cornua separated anteriorly, begin 10 mm behind glottis; cornua separated anteriorly by 1.5 mm, posteriorly by 14.5 mm; right cornu 16 mm, left cornu 17 mm. Body length 703 mm.

Eunectes gigas (CNHM 30954). Anterior ends separated, apparently due to injury which makes specimen incomplete. Cornua begin 16 mm behind glottis. Body length 900 mm.

Liasis albertisii (CNHM 13874). Cornua joined anteriorly; arch begins 8 mm anterior to 1st ventral, ends 6th ventral; arch 6 mm wide; cornua separated posteriorly by 4 mm; right cornu 17 mm, left cornu 16.5 mm. Body length 392 mm.

Liasis childreni (CNHM 75120). Cornua joined by a rounded arch 11.5 mm behind mental; arch 1 mm wide; cornua separated posteriorly by 8 mm; hyoid median length 13 mm. Body length 520 mm.

Lichanura roseofusca (CNHM 21568). Cornua separate, begin 13 mm behind glottis, end 4th ventral; cornua separated anteriorly by 3 mm; hyoid median length 16 mm. Body length 830 mm.

Loxocemus sumichrasti. Cornua joined as a pointed arch 18 mm behind mental; cornua end 46.5 mm behind mental; right cornu 30 mm, left cornu 31 mm; cornua separated posteriorly by 20 mm. Body length 794 mm.

Nardoana boa (CNHM 13834). Cornua joined by a rounded arch 13 mm behind glottis; cornua end 7th ventral; arch 1.5 mm wide; right cornu 23 mm. Body length 785 mm.

Python regius (CNHM 20812). Cornua separate, begin 22 mm behind mental, end 3rd ventral; cornua separated anteriorly by .5 mm, posteriorly by 7.5 mm; cornua 23 mm long. Body length 742 mm.

Sanzinia madagascariensis (CNHM 18286) (Fig. 1, L). Cornua separate (also in a second specimen); cornua begin 15 mm behind mental, end 4th ventral; cornua separated anteriorly by 1 mm; hyoid median length 15 mm. Body length 480 mm.

Trachyboa boulengeri (CNHM 78106). Cornua joined anteriorly and parallel with a process 2.5 mm long, 8 mm behind mental; hyoid ends 6th ventral; hyoid .5 mm wide, 11 mm long. Body length 240 mm.

Tropidophis maculatus (USNM 56328) (Fig. 15, A). Cornua joined and parallel with a process 1.5 mm long, 6.5 mm behind mental; hyoid begins 3 scales before 1st ventral, ends 9th ventral; hyoid 1 mm wide, 15 mm long. Body length 324 mm.

Ungaliophis continentalis (CNHM 19397). Cornua separate, begin 9.5 mm behind mental, end 6th ventral; cornua separated anteriorly by 1.5 mm, posteriorly by 2.5 mm; cornua 9.5 mm long. Body length 441 mm.

COLUBRIDAE (parallel type)

Achalinus spinalis (CNHM 18775). No process; begins 3rd ventral, ends 11th; hyoid 1 mm wide, 13 mm long. Body length 340 mm.

Achrochordus javanicus (USNM 20412) (Fig. 15, B). No process (also true in another examined specimen); hyoid begins 15 mm behind glottis; hyoid 3 mm wide anteriorly, cornua converge posteriorly; hyoid 92.5 mm long. Body length 1185 mm.

Adelphicos veraepacis nigrilatus (UI 6254). No process; hyoid begins 2nd ventral, ends 16th; hyoid 1 mm wide, 17 mm long. Body length 210 mm.

Amblycephalus kuangtungensis (CNHM 24489). A long, heavy process 1.5 mm; hyoid begins one scale before 1st ventral, ends 23rd; hyoid 1 mm wide, 45 mm long. Body length 430 mm.

Amblycephalus stanleyi (CNHM 24990). A long, tapering process

2.5 mm, near level of glottis; hyoid 1 mm wide, 21.8 mm long. Body length 183 mm.

Aparallactus capensis (CNHM 17710). Process 1 mm, begins 8 mm behind mental; hyoid 1 mm wide, 18 mm long, ends 18th ventral. Body length 207 mm.

Apostolepis quinquelineata (CNHM 26665). Process .5 mm, begins 8 mm behind mental; hyoid 1 mm wide, 16 mm long, ends 16th ventral. Body length 277 mm.

Atretium schistosum (MCZ 1330) (Fig. 15, C). Process 1 mm; hyoid begins 1st ventral, ends 20th; hyoid 1 mm wide, 35 mm long. Body length 340 mm.

Boiga dendrophila latifasciata. No distinct process, but arch is sharp; arch begins one ventral's width before 1st ventral, ends 16th ventral; hyoid 4.5 mm wide, 51.5 mm long. Body length 1120 mm.

Carphophis amoena vermis. No distinct process; arch lies 3 mm behind glottis; hyoid ends 20th ventral; hyoid 1 mm wide, 18 mm long. Body length 149 mm.

Cerberus rhynchops (Fig. 4, D). Two specimens examined with very distinctive hyoids. In CNHM 41117, process is very long, 10.5 mm; process is 1 mm wide at arch then widens to 1.5 mm before tapering to the apex; point of process 15 mm behind glottis, hyoid ends 12th ventral; hyoid 2 mm wide, 37 mm long. Body length 644 mm.

In another specimen, process is also very long, 5 mm; base of process formed of two convex rods which diverge 2 mm from basihyal to be 1 mm apart; then rods join and single process tapers to point; point 7 mm behind glottis; arch heavy, 1.5 mm wide; hyoid 1.5 mm wide, 23.5 mm long, ends 9th ventral. Body length 466 mm.

Chersodromus liebmanni. A small, sharp process, at 3rd ventral; hyoid ends 26th; hyoid 1 mm wide, 29.5 mm long. Body length 168 mm.

Chersydrus granulatus (Fig. 4, H). No process in two specimens; one set of measurements given. In CNHM 41118, rounded arch at level of glottis; hyoid 1.5 mm wide, 17 mm long; ends of cornua nearly touch. Body length 493 mm.

Chrysopelea ornata (CNHM 29165). Process rather triangular, .5 mm long, 19 mm behind mental; hyoid 1.2 mm wide, 29 mm long, ends 16th ventral. Body length 626 mm.

Clelia clelia. Two specimens examined, process only indicated; one set of measurements given. In CNHM 25414, point 13 mm behind mental; hyoid 50 mm long, ends 23rd ventral. Body length 500 mm.

Coluber c. constrictor. A very small process, begins 2nd ventral; hyoid ends 16th ventral; hyoid 3 mm wide, 63 mm long. Body length 958 mm.

Coluber c. flaviventris. A very short process, 1.5 mm, begins 2nd ventral; hyoid ends 16th ventral; hyoid 3.5 mm wide, 60 mm long. Body length 940 mm.

Coluber c. priapus (Fig. 4, F). A short, thick process, 2 mm, at 2nd ventral; hyoid 4 mm wide, 68 mm long, ends 21st ventral. Body length 740 mm.

Coniophanes imperialis copei. A sharp, triangular process, 1 mm, lies 11.5 mm behind mental at 2nd ventral; hyoid 1 mm wide, 30 mm long, ends 20th ventral. Body length 259 mm.

Coniophanes i. proterops (CNHM 21890). A slender process, 2 mm, lies 16 mm behind mental; hyoid 1.5 mm wide, 42 mm long, ends 19th ventral. Body length 349 mm.

Conopsis lineatus concolor (CNHM 49347). A long, tapering process, 3 mm, at 1st ventral; hyoid 2 mm wide, 47 mm long, ends 16th ventral. Body length 684 mm.

Conopsis biserialis. No process, arch rounded; hyoid begins 2nd ventral, ends 17th; hyoid 2 mm wide, 20 mm long. No body measurement.

Crotaphopeltis h. hotamboeia (CNHM 4037). A tapering process, 1.5 mm, 3rd ventral; hyoid 2 mm wide, 36 mm long, ends 19th ventral. No body measurement.

Cyclagras gigas. No process, arch rounded; hyoid begins two scales before 1st ventral, ends 16th ventral; hyoid 2 mm wide, 36 mm long. No body measurement.

Dasypeltis scaber. Two specimens examined with a long process; in CNHM 12841, process 2.7 mm, 1 mm behind glottis; hyoid 2 mm wide; hyoid cut 28 mm behind arch. Body length 439 mm.

In another specimen, process 2.5 mm; hyoid begins one scale before 1st ventral, ends 17th; hyoid 1 mm wide, 34 mm long. No body measurement.

Dendrophidion vinitor. A long, slender process enlarged at tip, 2 mm; hyoid begins 1st ventral, ends 13th; hyoid 2.5 mm wide, 55 mm long. Body length 549 mm.

Diadophis punctatus arnyi. A tapering process, 1 mm; hyoid begins 1st ventral, ends 18th; hyoid 1 mm wide, 15 mm long. Body length 119 mm.

Diadophis punctatus edwardsii (Fig. 4, C). Two specimens examined

with distinct process; one set of measurements given. Process 1 mm, 1.5 mm before 1st ventral; hyoid 1.5 mm wide, 29 mm long, ends 19th ventral. Body length 340 mm.

Dipsadoboa unicolor (CNHM 19459). Distinct, pointed process, 1 mm, lies 13 mm behind mental; hyoid 1.5 mm wide, 39 mm long, ends 17th ventral. Body length 607 mm.

Dispholidus typus (CNHM 48081). A blunt process, 2 mm, at 1st ventral; hyoid 44 mm long, ends 16th ventral. Body length 1070 mm.

Dromophis lineatus. Long, slender process, 4.5 mm, 18 mm behind mental; hyoid 2 mm wide, 51 mm long, ends 16th ventral. Body length 648 mm.

Drymarchon corais erebennus. Triangular process, 1 mm, at 3rd ventral; hyoid 3 mm wide, 46.5 mm long, ends 20th ventral. Body length 405 mm.

Drymobius bifossatus. Process 3 mm, at scale before 1st ventral; hyoid 4 mm wide, 59 mm long, ends 13th ventral. Body length 1005 mm.

Drymobius m. margaritiferus. Long process, 1.8 mm, at 1st ventral; hyoid 3 mm wide, 80.5 mm long, ends 29th ventral. Body length 500 mm.

Dryophis mycterizans. No process, although arch thick; arch lies two scales before 1st ventral; hyoid 1.5 mm wide, 25 mm long, ends 6th ventral. Body length 1000 mm.

Elaphe guttata (Fig. 4, A). Long process, 3.5 mm, at 1st ventral; hyoid 3.5 mm wide, 63 mm long, ends 15th ventral. Body length 1001 mm.

Elaphe laeta. Small process, 1 mm, at 1st ventral; hyoid 2 mm wide, 23 mm long, ends 15th ventral. Body length 351 mm.

Elaphe o. obsoleta. Blunt process, 2 mm, at scale before 1st ventral; hyoid 3 mm wide at arch, 7 mm wide at middle, 52 mm long, ends 13th ventral. Body length 1209 mm.

Elaphe vulpina. Short process, 1.5 mm, 5 mm before 1st ventral; hyoid 2 mm wide, 38.5 mm long, ends 11th ventral. Body length 788 mm.

Elapomorphus nuchalis. Two specimens examined with very short process; one set of measurements given. In CNHM 9028, process .1 mm, 9 mm behind mental; hyoid 1 mm wide, 14 mm long, ends 14th ventral. Body length 214 mm.

Elapops modestus. Small, angular process, 1 mm, at 3rd ventral; hyoid 2 mm wide, 38 mm long, ends 24th ventral. Body length 337 mm.

Enhydryis enhydryis. Very long process, 9 mm, at nine scales before 1st ventral; hyoid 1 mm wide, 39.5 mm long, ends 13th ventral. Body length 475 mm.

Enhydryis plumbea. Three specimens examined have a long, thin process; two measurements given. In CNHM 6686, process 1.5 mm, 12.5 mm behind mental; hyoid 1.5 mm wide, 21.5 mm long. Body length 342 mm.

In CNHM 11552, process 5 mm, 8 mm behind glottis; hyoid 1 mm wide, 48 mm long. Body length 374 mm.

Enulius unicolor. Short, sturdy process, .5 mm, at 2nd ventral; hyoid 1 mm wide, 19.5 mm long, ends 24th ventral. Body length 209 mm.

Farancia a. abacura. Sturdy, long process, 4 mm, at 2.5 mm before 1st ventral; hyoid 2 mm wide, 34 mm long, ends 10th ventral; cornua heavy. Body length 890 mm.

Farancia a. reinwardtii (Fig. 4, E). Strong process, 4 mm, at 1st ventral; hyoid 3 mm wide, 41 mm long, ends 12th ventral. Body length 746 mm.

Ficimia publia (UI 33650). Large process, 1 mm, at 1st ventral; hyoid 3 mm wide, 48 mm long, ends 15th ventral. Body length 410 mm.

Fimbrios klossi (CNHM 71701). Small process, .5 mm, at 6th ventral; hyoid 1 mm wide, 14.5 mm long, ends 15th ventral. Body length 295 mm.

Geophis semidoliatus (UI 25952). No process, arch rounded, at 3rd ventral; hyoid .5 mm wide, 27 mm long, ends 22nd ventral. No body measurement.

Haldea striatula. No process, rounded arch, at 3rd ventral; hyoid 1 mm wide, 15 mm long, ends 17th ventral. Body length 147 mm.

Haldea valeriae elegans. No process, arch rounded, at 2nd ventral; hyoid 1 mm wide, 22.5 mm long, ends 19th ventral. Body length 111 mm.

Haplopeltura boa (CNHM 63605). Long, heavy process, 3 mm, 11 mm behind mental; hyoid 1 mm wide, 33 mm long. Body length 460 mm.

Heterodon n. nasicus. No process, arch rounded, at 1st ventral; hyoid 3.5 mm wide, 49.5 mm long, ends 18th ventral. Body length 450 mm.

Heterodon p. platyrhinos (Fig. 16, A). No process, but arch angular, lies 15 mm behind glottis at 1st ventral; hyoid 4 mm wide, 58 mm long, ends 15th ventral. Body length 596 mm.

Homalopsis buccata (CNHM 11551). Long, slender process, 5.5 mm, at 2nd ventral; hyoid 2 mm wide, 54.5 mm long, ends 18th ventral. Body length 755 mm.

Lampropeltis calligaster. Small process, 1.5 mm, at 1st ventral; hyoid 3 mm wide, 51.5 mm long, ends 14th ventral. Body length 979 mm.

Lampropeltis d. doliata (Fig. 4, B). No actual process, arch angular, at 1st ventral; hyoid 4.5 mm wide, 49 mm long, ends 17th ventral. Body length 825 mm.

Lampropeltis e. elapsoides. Small process, 1 mm, at 1st ventral; hyoid 1.5 mm wide, 38.5 mm long, ends 22nd ventral. Body length 390 mm.

Lampropeltis getulus holbrooki. No process, arch rounded, lies 2 mm before 1st ventral; hyoid 1.5 mm wide, 36 mm long, ends 17th ventral. Body length 409 mm.

Lampropeltis getulus splendida. Two specimens examined. In one specimen, a small process, .5 mm, at 1st ventral; hyoid 2 mm wide, 25.5 mm long, ends 19th ventral. Body length 310 mm.

In other specimen, no process, arch rounded, at 2nd ventral; hyoid 4.5 mm wide, 70.5 mm long, ends 21st ventral. Body length 957 mm.

Lampropeltis knoblochi. Small triangular process, .5 mm, at two scales before 1st ventral; hyoid 1.5 mm wide, 39.5 mm long, ends 16th ventral. Body length 630 mm.

Leptodeira maculata. Large, tapering process, 2 mm, at scale before 1st ventral; hyoid 3 mm wide, 53.5 mm long, ends 25th ventral. Body length 410 mm.

Leptodeira septentrionalis polysticta. Short, tapering process, 1.5 mm, at 1st ventral; hyoid 1.5 mm wide, 53 mm long, ends 35th ventral. Body length 660 mm.

Leptophis diplotropis. Large, sturdy process, 2 mm, at 1st ventral; hyoid 2.5 mm wide, 37 mm long, ends 14th ventral. Body not measured.

Leptophis m. mexicanus. Process 1 mm, at 2nd ventral; hyoid 1.5 mm wide, 38 mm long. Body length 595 mm.

Manolepis putnami. Long, tapering process, 1 mm, at two scales before 1st ventral; hyoid 2 mm wide, 32 mm long, ends 13th ventral. Body not measured.

Masticophis f. flagellum. No process, rounded arch at 3rd ventral; hyoid 3 mm wide, 52 mm long, ends 14th ventral. Body length 1142 mm.

Masticophis f. flavigularis. Small, pointed process, 2 mm, at 2nd

ventral; hyoid 5 mm wide, 59 mm long, ends 14th ventral. Body length 1246 mm.

Mehelya nyassae (CNHM 77612). Long process, 2.5 mm, at 1st ventral; hyoid 3 mm wide, 55 mm long, ends 26th ventral. Body length 510 mm.

Natrix cyclopion floridana. No process, rounded arch at 8.5 mm before 1st ventral; hyoid 4 mm wide, 57.5 mm long, ends 11th ventral. Body length 768 mm.

Natrix e. erythrogaster. No process, rounded arch at 2nd ventral; hyoid 2 mm wide, 58 mm long, ends 17th ventral. Body length 686 mm.

Natrix grahami. Short, distinct process, 1 mm, at 1st ventral; hyoid 1 mm wide, 42 mm long, ends 18th ventral. Body length 422 mm.

Natrix piscator. Short, pointed process, 1 mm, at 2nd ventral; hyoid 3.5 mm wide, 56 mm long, ends 19th ventral. Body not measured.

Natrix septemvittata (UI 16282). No process, rounded arch at 2nd ventral; hyoid 2 mm wide, 39 mm long, ends 18th ventral. Body length 525 mm.

Natrix sipedon confluens. No process, angular arch at 1st ventral; hyoid 2 mm wide, 35 mm long, ends 18th ventral. Body length 443 mm.

Ninia d. diademata. No process, rounded arch at 3rd ventral; hyoid 1.5 mm wide, 25 mm long, ends 27th ventral. Body length 198 mm.

Ninia sebae morleyi. No process, rounded arch at 3rd ventral; hyoid 2 mm wide, 32 mm long, ends 24th ventral. Body not measured.

Nothopsis rugosus (CNHM 77604). Small process, 1 mm, at 3rd scale before 1st ventral; hyoid 1 mm wide, 26 mm long, ends 19th ventral. Body length 295 mm.

Ophedrys aestivus. No process, arch angular at 1st ventral; hyoid 1 mm wide, 32 mm long, ends 16th ventral. Body length 421 mm.

Ophedrys vernalis (Fig. 3, B). No process, angular arch at 2 mm before 1st ventral; hyoid 2 mm wide, 35.5 mm long, ends 16th ventral. Body length 390 mm.

Oxybelis acuminatus. In two specimens examined, process and arch triangular; one set of measurements given. Process .5 mm, at scale before 1st ventral; hyoid 1 mm wide, 18.5 mm long, ends 8th ventral. Body length 745 mm.

Oxyrhabdinium leporinum. No process, rounded arch at 5th ventral; hyoid 1.5 mm wide, 27.5 mm long, ends 16th ventral. Body length 472 mm.

Pituophis catenifer sayi. No process in two specimens; one set of

measurements given. In UI 39637, arch at 1st ventral; hyoid 4 mm wide, 37 mm long, ends 13th ventral. Body length 870 mm.

Psammodynastes pulverulentus. No process, rounded arch at scale before 1st ventral; hyoid 1.5 mm wide, 24.5 mm long, ends 17th ventral. Body length 300 mm.

Rhadinaea flavilata (Fig. 4, J). Tapering process, 1 mm, 1 mm before 1st ventral; hyoid 1.5 mm wide, 32 mm long, ends 19th ventral. Body length 238 mm.

Rhadinaea laureata. Process .5 mm, at scale before 1st ventral; hyoid 2 mm wide, 39.5 mm long, ends 24th ventral. Body length 310 mm.

Rhadinella schistosa. Small process, at 1st ventral; hyoid .5 mm wide, 15 mm long, ends 19th ventral. Body length 179 mm.

Rhinocheilus lecontei tessellatus. Small process, teatlike, 15 mm, at two scales before 1st ventral; hyoid 2.5 mm wide, 50.5 mm long. Body length 637 mm.

Salvadora grahamiae hexalepis (Fig. 3, H). Long, tapering process, 5 mm, at 1st ventral; hyoid 1.5 mm wide, 38.5 mm long, ends 17th ventral. Body length 675 mm.

Salvadora intermedia richardi. Long, tapering process, 2.5 mm, at scale before 1st ventral; hyoid 1.5 mm wide, 35 mm long, ends 17th ventral. Body length 553 mm.

Salvadora mexicana. Long, sharply tapering process, 2 mm, at scale before 1st ventral; hyoid 3 mm wide, 43 mm long, ends 14th ventral. Body length 760 mm.

Sibynomorphus catesbyi (CNHM 35711). (Fig. 3, D). No process, rounded arch 3 mm behind glottis; hyoid 1.5 mm wide, 49.5 mm long. Body length 422 mm.

Sibynophis collaris (CNHM 71708). Sharply tapering process, 2 mm, at 2nd ventral; hyoid 1 mm wide, 31.5 mm long, ends 23rd ventral. Body length 360 mm.

Sonora o. occipitalis (see Fig. 3, G). Process 1 mm, at 1st ventral; hyoid 1 mm wide, 20 mm long, ends 18th ventral. Body length 230 mm.

Sonora taylori. Small process, .5 mm, at two scales before 1st ventral; hyoid .5 mm wide, 18 mm long, ends 18th ventral. Body length 194 mm.

Stilosoma extenuatum. Large, sharp process, .5 mm, at 1st ventral; hyoid 1 mm wide, 15.5 mm long, ends 11th ventral. Body length 410 mm.

Storeria dekayi (Fig. 3, C). Two specimens examined, without process; one set of measurements given. Rounded arch at 2nd ventral; hyoid 1 mm wide, 21 mm long, ends 22nd ventral. Body length 138 mm.

Tantilla gracilis (Fig. 3, F). Tapering process, .5 mm, at 1st ventral; hyoid 1 mm wide, 15.5 mm long, ends 18th ventral. Body length 138 mm.

Thamnophis eques. No process, rounded arch at scale before 1st ventral; hyoid 1.5 mm wide, 62 mm long, ends 20th ventral. Body length 582 mm.

Thamnophis elegans vagrans (Fig. 16, C). No process, rounded arch at 1st ventral; hyoid 3 mm wide, 50 mm long, ends 18th ventral. Body length 600 mm.

Thamnophis melanogaster canescens (UI 18875). Process bluntly triangular, 1 mm, at scale before 1st ventral; hyoid 1.5 mm wide, 30 mm long, ends 14th ventral. Body length 395 mm.

Thamnophis s. scalaris. Small, triangular process, .5 mm, at 1st ventral; hyoid 2.5 mm wide, 33 mm long, ends 18th ventral. Body length 326 mm.

Toluca l. lineata. No process, arch angular at 1st ventral; hyoid 1.5 mm wide, 26 mm long, ends 18th ventral. Body length 199 mm.

Trimorphodon b. biscutatus. Long, tapering process, 2 mm, at two scales before 1st ventral; hyoid 2 mm wide, 36 mm long, ends 17th ventral. Body length 713 mm.

Tropidoclonion lineatum. No process, arch angular, at 4th ventral; hyoid 1.5 mm wide, 21.5 mm long, ends 24th ventral. Body length 159 mm.

Tropidonotus natrix (Fig. 3, E). No process, rounded arch at 1st ventral; hyoid 2 mm wide, 46.5 mm long, ends 20th ventral. Body length 452 mm.

Xenodermus javanicus (CNHM 67247). Short process, .5 mm, at 11 mm behind mental; hyoid 1 mm wide, 59 mm long; a relatively long hyoid. Body length 500 mm.

ELAPIDAE (parallel type)

Acanthophis antarctica (CNHM 13871). Process and arch triangular, 14 mm behind mental; hyoid 3.5 mm wide, 31 mm long. Body length 328 mm.

Aspidelaps scutatus. Small process, 11 mm behind mental; hyoid 3.5 mm wide, 40 mm long. Body length 392 mm.

Bungarus multicinctus (CNHM 25166). Process 2 mm, 10 mm behind mental; hyoid 2 mm wide, 33 mm long. Body length 642 mm.

Calliophis macclellandii (CNHM 6659). Long process, 1 mm, 7 mm behind mental; hyoid 1 mm wide, 20 mm long. Body length 390 mm.

Demansia nuchalis (CNHM 15884). No process, angular arch 15.5 mm behind mental; hyoid 2 mm wide, 47 mm long. Body length 916 mm.

Dendraspis viridis (CNHM 44385). Process 2 mm, 18 mm behind mental; hyoid 2 mm wide, 35 mm long. Body length 1210 mm.

Denisonia woodfordi (CNHM 13834). Long process, 2.5 mm, 17.5 mm behind mental; hyoid 2 mm wide, 33 mm long, ends 12 ventral. Body length 618 mm.

Doliophis bilineatus (CNHM 53555). Angular process, 1 mm, 9 mm behind mental; hyoid 21 mm long. Body length 479 mm.

Elaps lacteus (CNHM 17717). Process 1 mm, at 5th ventral; hyoid 17 mm long, ends 21st ventral. Body length 229 mm.

Elapsoidea sundervalli fitzsimonsi (CNHM 17667). Tapering process, 1 mm, 12.5 mm behind mental; hyoid 2 mm wide, 54 mm long, ends 19th ventral. Body not measured.

Furina annulata (CNHM 29114). Long, slender process, 2 mm, 9 mm behind mental; hyoid 1.5 mm wide, cornua 17 mm long but incomplete. Body length 549 mm.

Hemachatus hemachates. No process, arch flat in two specimens; one set of measurements given. In CNHM 17663, arch 11.5 mm behind mental; hyoid 2 mm wide, 30 mm long, ends 15th ventral. Body length 285 mm.

Hemibungarus kelloggi (CNHM 24999). Long, slender process, 1.5 mm, 9 mm behind mental; hyoid 2 mm wide, 25.5 mm long, ends 13th ventral. Body length 485 mm.

Leptomicrurus narducci (CNHM 27081). Short process, .5 mm, 8 mm behind mental; hyoid 1 mm wide, 12 mm long, ends 11th ventral. Body length 422 mm.

Maticora bivirgata (CNHM 30546). Short process, 1 mm, 14 mm behind mental; hyoid 2 mm wide, 51 mm long, ends 20th ventral. Body length 1030 mm.

Micropechis ikaheka (CNHM 13937). Process 3 mm, at 1st ventral; hyoid 3 mm wide, 50 mm long, ends 14th ventral. Body not measured.

Micruroides euryxanthus (CNHM 48526). Short process, 1 mm, at 4th ventral; hyoid 1.5 mm, 22 mm long, ends 21st ventral. Body length 349 mm.

Micrurus a. affinis. Long, triangular process, 3 mm, at 2nd scale before 1st ventral; hyoid 1 mm wide, 27 mm long, ends 16th ventral. Body length 430 mm.

Micrurus fulvius (Fig. 3, H). Two specimens examined, with short process; one set of measurements given. Process 1 mm, at 1st ventral; hyoid 2.5 mm wide, 35.5 mm long, ends 18th ventral. Body length 560 mm.

Naja naja samarensis (CNHM 53542). Process only indicated, 14 mm behind mental; hyoid 5.5 mm wide, 39 mm long. Body length 766 mm.

Notechis scutatus (CNHM 15800). Triangular process, 3.5 mm, 14.5 mm behind mental; hyoid 4 mm wide, 45 mm long. Body length 788 mm.

Ogmodon vitianus (CNHM 22999). Hyoid damaged anteriorly; hyoid ends 11th ventral. Body length 128 mm.

Pseudelaps mulleri (CNHM 14200). Large process, 2.3 mm, 8 mm behind mental; hyoid 1 mm wide, 16 mm long. Body length 344 mm.

Utrocalamus prussi (CNHM 43030). Long process, 2 mm, 11 mm behind mental; hyoid 1 mm wide, 10 mm long, ends 5th ventral. Body length 630 mm.

HYDROPHIDAE (parallel type)

Aipysurus eydouxii. Two specimens examined, with long process; one set of measurements given. In CNHM 11572 (Fig. 17, B), process 4 mm, at eight scales before 1st ventral; hyoid 1.5 mm wide, 28 mm long, ends 7th ventral. Body length 460 mm.

Hydrophis cyanocinctus (CNHM 28311). Long, sharply tapering process, 4.5 mm, 8 mm behind mental; hyoid 2 mm wide, 17.5 mm long. Body length 522 mm.

Kerilia jerdonii. Long, slender process, 5 mm, 10 mm behind mental; hyoid 2 mm wide, 17 mm long. Body length 763 mm.

Lapemis hardwicki (CNHM 11583). Long, slender process, 5 mm, 11 mm behind glottis; hyoid 2.5 mm wide, 34 mm long. Body length 650 mm.

Laticauda colubrina (CNHM 4047). Long, slender process, 4.5 mm, 3 mm behind glottis; hyoid 1.5 mm wide, 27 mm long. Body length 740 mm.

Pelamis platurus. Two specimens examined, process long and slender. In CNHM 40468, process 2 mm plus (tip broken), about 13 mm behind

mental; hyoid 1.5 mm wide, 15 mm long, ends 6th ventral. Body length 415 mm.

In CNHM 41591, process 3 mm, at scale before 1st ventral; hyoid 2.5 mm wide, 18.5 mm long, ends 3rd ventral. Body length 542 mm. Cornua abnormal: do not attach to hyoglossal muscles, but bow out on either side to end independent of muscles.

Thalassophina viperina (CNHM 11567). Process broken; hyoid 1 mm wide, ends 7th ventral. Body length 325 mm.

VIPERIDAE (parallel type)

Aspis cerastes (CNHM 41596). Long process, 4 mm, 22 mm behind mental; hyoid 2 mm wide, 29 mm long. Body length 539 mm.

Atheris nitschei (CNHM 9901). No process, rounded arch at 19.5 mm behind mental; hyoid 2 mm wide, 25 mm long. Body length 535 mm.

Atractaspis microlepidota (CNHM 375). Very long process, 4.5 mm, 14 mm behind mental; hyoid 1.5 mm wide, 40 mm long, ends 21st ventral. Body length 225 mm.

Bitis cornutus (CNHM 16039). Short process, .5 mm, 10 mm behind mental; hyoid 2.5 mm wide, 35 mm long. Body length 326 mm.

Bitis nasicornis (CNHM 12820). No process, rounded arch 23 mm behind mental; hyoid 6 mm wide, 57 mm long. Body length 703 mm.

Causus rhombeatus (CNHM 12969). No process, rounded arch 8.5 mm behind mental; hyoid 2 mm wide, 36 mm long. Body length 457 mm.

Cerastes vipera. Two specimens examined, with long process; one set of measurements given. In CNHM 63115 (Fig. 17, C), process 3.5 mm, at two scales before 1st ventral; hyoid 1 mm wide, 28 mm long, ends 13th ventral. Body length 460 mm.

Echis carinatus (CNHM 18215). Long process, 3.5 mm, 13.5 mm behind mental; hyoid 2 mm wide, 30 mm long. Body length 404 mm.

Pseudocerastes fieldi (CNHM 11062). No process, rounded arch 16 mm behind mental; hyoid 1.5 mm wide, 33 mm long. Body length 550 mm.

Vipera berus. Long process, 2 mm, at 1st ventral; hyoid 1.5 mm wide, 22 mm long, ends 15th ventral. Body length 271 mm.

CROTALIDAE (parallel type)

Agkistrodon contortrix. Very short process, 1 mm, at 2nd ventral; hyoid 3 mm wide, 48 mm long, ends 18th ventral. Body length 592 mm.

Agkistrodon p. piscivorus (UI 26861). Process 3 mm, at 4th ventral; hyoid 6 mm wide, 49 mm long, ends 14th ventral. Body length 895 mm.

Bothrops atrox. Long process, 5 mm, at 1st ventral; hyoid 5 mm wide, 65.5 mm long, ends 12th ventral. Body length 1515 mm.

Bothrops mexicanus (Fig. 1, M). Two specimens examined, with long processes; one set of measurements given. In USNM 123712, process 1.5 mm, at 1st ventral; hyoid 3 mm wide, 39 mm long, ends 13th ventral. Body length 589 mm.

Crotalus cerastes (UI 171). Long process, 3 mm, at scale before 1st ventral; hyoid 2.5 mm wide, 32 mm long, ends 13th ventral. Body length 495 mm.

Crotalus pricei pricei (CNHM 1459A). Large, triangular process, 2 mm, 16.5 mm behind mental; hyoid 3 mm wide, 34.5 mm long, ends 19th ventral, beyond termination of hyoglossi. Body length 413 mm.

Crotalus tigris. Long, triangular process, 4 mm, 4 mm before 1st ventral; hyoid 3.5 mm wide, 54.5 mm long, ends 18th ventral. Body length 646 mm.

Lachesis muta (CNHM 22991). Process 4 mm, at 3rd ventral; hyoid 6 mm wide, 53 mm long, ends 15th ventral. Body incomplete, but very large.

Sistrurus miliarius. Long, tapering process, 3.5 mm, at 1st ventral; hyoid 2 mm wide, 37 mm long, ends 17th ventral. Body length 421 mm.

Sistrurus ravus. Triangular process, 2 mm, at scale before 1st ventral; hyoid 3.5 mm wide, 46.5 mm long, ends 15th ventral. Body length 547 mm.

Trimeresurus wagleri (CNHM 53564). Long process, 2.5 mm, 34 mm behind mental; hyoid 1.5 mm wide, 39 mm long. Body length 562 mm.

D. Discussion

Variations. The variations discovered within any one morphological group were not remarkable, and in any case they merely represented some reduction or variant of the basic form. None of the variations are considered to have adaptive value.

In the anomalepidids, no particular variations were noted in the few specimens examined. The median hyoid length/body length ratio is about 1 per cent.

For the "Y" type hyoid in typhlopids a certain number of variations

have been described, chiefly by List (1966). He has illustrated three forms of the hyoid: (1) a complete Y shape, (2) complete except that the cornua are disconnected from the basihyal, and (3) hyoid composed only of the two separated cornua. His preparations were stained specimens. The author has examined specimens with forms (1) and (3). In any case, the basic typhlopoid type is one with a basihyal and attached 1st ceratobranchial cornua. The straight length of the hyoid is less than 1 per cent of the body length. The hyoid is all or partly bony in some species.

No particular variations were found in the "Y" type hyoid of leptotyphlopids. The basihyal and attached 1st ceratobranchials are considered to be present, just as in the basic typhlopoid hyoid. The leptotyphlopoid hyoid is longer relatively, being about 2 per cent of the body length.

Uropeltids have the "V" type hyoid, modified by the 1st ceratobranchial cornua being separated at their anterior ends; no basihyal is considered present. The hyoid is relatively small; the length of the cornua tends to be about 2 per cent of the body length. The cornua usually begin opposite the 1st ventral and the end around the 5th. Among the examined species, *Rhinophis planiceps* has the most reduced hyoid.

Aniliids also have the "V" type hyoid. The new world genus *Anilius* has a complete type, with the 1st ceratobranchial cornua united anteriorly; no lingual process or other enlargement at the union is present. The hyoid has a straight length of about 2 per cent of the body length. In the old world genus *Cylindrophis* the cornua are reduced and separate, and are about 1.5 per cent of the body length. *C. maculatus*, in particular, has very slender and markedly reduced cornua, lying on the lateral aspect of the posterior part of the *hyoglossi*.

The well-formed "V" type hyoid of *Xenopeltis* is about 3 per cent of the body length, and extends from about the 1st ventral to the 11th.

In the Boidae (*sensu stricto*) the cornua are of the "V" type and may or may not be joined anteriorly, and there does not seem to be any correlation of this variation with the pythons and boas. In general the cornua are always well developed among boids, even if not joined; and in those cases where there is no union, the anterior separation is never great. The median hyoid length is up to 4 per cent of the body length.

The parallel type hyoid is always well developed and always has the cornua joined anteriorly. The boidlike genera *Tropidophis*, *Trachyboa*, *Casarea*, and *Bolyeria* have a parallel type hyoid and always have a distinct lingual process as well. In fact, this hyoid resembles closely the hyoid of any number of colubrids and elapids, etc. In *Tropidophis*, where the hyoid has been investigated in several species — *maculatus*,

melanurus, and *pardalis* — the hyoid is at least 4.5 per cent of the body length; the percentage is similar for *Trachyboa*. The significance of the parallel type hyoid in these four genera is puzzling. About the only point that can be made at this time is that these genera probably represent a group that early diverged from the main body of boids with their hyoid form paralleling that of the rest of the snakes with the same kind of hyoid.

For the families Colubridae, Elapidae, Hydrophidae, Viperidae, and Crotalidae, there is noticeable variation in the lingual process. Usually the process is tapered when long, and stubby when short, often with a rounded, expanded tip. The process may also be triangular in form; in this case it is difficult to tell whether this really constitutes a true process of the basihyal, the basihyal itself, or merely the shape of the fusion of the cornua with the basihyal elements missing. The cornua form a smooth continuous arch in front in many species. All basihyal elements are probably missing in these cases.

The length of the process, and indeed, the presence of the process, is liable to variation in some genera. Among the colubrids examined an arbitrary inspection shows that there are approximately equal numbers of genera without processes, with small ones (roughly 3-4 per cent of the hyoid total length), and with well-developed ones (more than 4 per cent). Genera in which two or more specimens of a species, or several species, were examined, and which show two or more conditions, are *Coniophanes*, *Lampropeltis*, and *Elaphe* (all small, large); and *Masticophis*, *Natrix*, and *Thamnophis* (all none, small). It would seem from this admittedly limited sample that if a genus has a species with a long process, the genus does not have species with none at all. The sample is not large enough to justify a flat statement, of course, but the trend is at least suggested.

The longest processes seen in the colubrids belong to *Cerberus* and *Enhydryis*. The former has the process 20-30 per cent of the hyoid length, and the latter up to at least 22 per cent. In *Salvadora grahamiae* and *Farancia* the process is at least 12 per cent. In *Cerberus* the lingual process is the most ornate among snakes; it is long, heavy, and in two cases, with a prominent swelling (Fig. 4, D). A third specimen lacks the swelling, although the process and the arch are heavy.

It is possible that the basihyal may either be reduced or else absent in certain genera, e.g., *Masticophis*, *Natrix*, *Thamnophis*, as noted above. These examples, together with other colubrid genera having smooth, rounded arches, possibly show that there is a trend toward loss of the basihyal thereby reducing the hyoid to the pair of 2nd ceratobranchials.

The elapids are much more consistent in the presence of a lingual process than the colubrids. Nearly every elapid genus has been examined, and results show that the process is present in every genus examined save *Hemachatus*, an African cobra. In this species Pringle (1954) studied the embryonic development and noted that apparently no basihyal formed. The arch is rounded and smooth in the adult, which substantiates Pringle's view. About one-half of the elapid genera have a process that can be considered long. In *Urocalamus* the process is about 19 per cent of the hyoid length; this seems to be the relatively longest process among elapids.

In the six genera of hydrophids examined, there is a very long process in every case, ranging from 14 to 28 per cent of the hyoid length. A specimen of *Kerilia jerdonii* has the longest one, relatively speaking (28 per cent). It is hard to see a particular, functional advantage in a long process, since in snakes it provides no special support for the tongue, despite the name.

Among the viperids there are four genera with species that have a very small lingual process (*Atheris*, *Bitis*, *Causus*, and *Pseudocerastes*), and five genera with species that have a noticeably large one (*Aspis*, *Atractaspis*, *Cerastes*, *Echis*, and *Vipera*). The relatively longest process is found in *Aspis*—14 per cent. *Bitis nasicornis* has a small process, whereas *B. cornutus* has none.

Among crotalids the lingual process is apparently always present; it is also generally well developed. Perhaps the longest one—10 per cent of the hyoid length—is found in the genus *Sistrurus*. In *Agkistrodon contortrix* the process is small and triangular; in *A. piscivorus* the process is long and prominent.

It might be concluded that, in general, the poisonous snake species tend to have a prominent lingual process, whereas the colubrid species show much more variation in size and presence of the process.

The cornua in the parallel type are generally longer relatively than in the "V" type. Whereas the hyoid is usually a little less than 4 per cent of the body length in the Boidae, the hyoid is usually at least 8 per cent of the body length, and often about 10 per cent in those families with a parallel type hyoid. There are, of course, exceptions, such as *Boiga* and *Chersydrus*, two colubrid genera which have a percentage of about 4 per cent. The longest hyoids relative to body length were found in: *Drymobius*, 16 per cent, *Chersodromus*, 17 per cent, *Atractaspis*, 18 per cent, *Natrix sipedon* (a juvenile), 19 per cent, and *Haldea valeriae*, 20 per cent. These are all colubrids except *Atractaspis*, a viperid.

Functions. The primary function of the hyoid is to provide a support

for the tongue muscles, the *hyoglossi*, which attach posteriorly to the cornua. Muscles from the mandibles also attach to the cornua in all snakes; also, there are muscles, of a variable number and identity in different species, which run from the skin, nape region, and the anterior ribs to the cornua. When these muscles act they tend to act in opposing sets and thereby hold the hyoid firm so that the *hyoglossi* may operate efficiently.

Gnanamuthu (1937) claimed that the cornua flex in the boa constrictor upon tongue protraction, and upon retraction elasticity returns the cartilage to normalcy and thus aids in withdrawing the tongue. In view of muscle relationships this does not seem likely. Moreover, in the parallel type it is difficult to believe that the cornual cartilages, lying along the longitudinally placed *hyoglossi*, are flexed upon protraction of the tongue. The only directions available for flexing would be dorsal or ventral, and this simply does not happen, as inspection and experimentation have shown. Surely the hyoid is fixed in position when the tongue is protracted and vibrated.

Phylogenetic Significance. It is not especially reasonable to derive a phylogenetic pattern from the morphological types of one structure. The hyoid in snakes is no exception. However, the hyoid types do have a certain value, and they certainly seem to indicate some sort of natural groupings.

The following discussion is based on the assumption that all modern snakes are monophyletic.

The basic, complete lizard hyoid is a good place to start: three pairs of cornua with a basihyal and its lingual process. It is altogether reasonable that the early snakes also had such a complete hyoid, and this idea is reinforced by the evidence already given — that all three pairs of cornua are present in modern snakes, but only one pair is present in any one family.

In looking over the modern lizards in hopes of finding traces of ancestry for the snakes, it is easy to fall prey to a fallacious line of reasoning: that modern lizards are necessarily like those ancestors which gave rise to snakes. After all, it is surely true that modern snakes have changed from their earlier relatives; so it might be as reasonably true that modern lizards have changed from theirs. Indeed, there is no living lizard, or even group of them, that can unquestionably be called related to the ancestors of snakes. Rather than select some group of lizards and positively work with it as a source for the snakes, the author prefers at this point merely to establish a likely basic pattern for the hyoid. Such a pattern might well be called primitive, and probably consisted of three pairs of cornua and the basihyal.

From early snakes with this pattern one event probably occurred quite early in the evolutionary scale — one group lost both the 1st and 2nd ceratobranchials, leaving a hyoid composed solely of 2nd arch components, the ceratohyals and hypohyals. This line of evolution has given us the Anomalepididae, which lack also a lingual process and perhaps any trace of the basihyal altogether.

The indication is that the remainder of the stock gave rise to forms that sooner or later lost the 2nd arch cornua, although retaining the basihyal and its lingual process. This hyoid would then be composed of a basihyal and process plus the 1st and 2nd ceratobranchials. Probably a fairly early diversion from this stock gave rise to a line which showed a loss of the 2nd ceratobranchials. From this line came the present-day Typhlopidae and Leptotyphlopidae. Their hyoids are very similar in basic form and are considered, of course, to be composed of the basihyal and process plus the 1st ceratobranchials.

The next event can well be considered to have been a loss of the 2nd ceratobranchials, and eventually also a loss of the basihyal elements. This group is represented by the present-day uropeltids, aniliids, xenopeltids, and boids (*sensu stricto*).

The remaining group of snakes eventually lost the 1st ceratobranchials entirely, and then had a hyoid composed of the 2nd ceratobranchials plus basihyal elements. From this group of snakes, the remaining modern families have descended — all of which have this parallel type of hyoid composed of a basihyal, which is secondarily lost in some species, plus what are considered to be 2nd ceratobranchials. Note that the boidlike genera *Bolyeria*, *Casarea*, *Trachyboa*, and *Tropidophis* also seem to fit into this line of evolution.

This phylogenetic pattern is no doubt artificial in many respects. However, in the overall sense, the four groups of the hyoid form in modern snakes do outline such a pattern. Later, in the second part of this work, the evidence of the musculature will modify this pattern, and the end result can be seen in Figure 19.

There have been several obvious trends in the evolution of the snake hyoid. (1) There has been a reduction in the number of cornua and a resultant simplification of the hyoid form. The four main groups, all with only one pair of cornua, which varies as to identity according to the group, are evidences of this. (2) The hyoids within the respective groups have also had a tendency to undergo further reduction or simplification. This is illustrated in many cases by the absence of the lingual process and by the apparent absence of the entire basihyal. In some typhlopids there may also have been a loss of cornua, as suggested by List (1966). (3) Ossification as a process has largely been

lost for the hyoids in snakes. Only in the Typhlopidae does ossification ever take place in the hyoid, and here apparently this occurs only in some species, and perhaps only in older specimens of these species.

It should be noted explicitly that none of the hyoids of modern snakes are at all primitive, but rather the opposite, being very much modified and altered by reduction into simple forms.

E. Summary

1. The basic complete lizard hyoid type is taken to be one composed of the basihyal plus lingual process, hypohyals and ceratohyals, 1st ceratobranchials, and 2nd ceratobranchials; these parts are derived from branchial arches 2, 3, 4. The 1st ceratobranchials are characteristically bony to some degree.

2. The hyoid in snakes is located on the ventral surface of the head and neck, generally just deep to the cutaneous layer of muscles. In the Typhlopidae, Leptotyphlopidae, and Anomalepididae the hyoid lies completely posterior to the head.

3. The hyoid of snakes is cartilaginous in all cases except in some examined species of typhlopids, where the hyoid may be partly or totally bony.

4. According to the shape of the hyoid, there are four seemingly natural major types definable: (1) "M" type; (2) "Y" type, or reduction thereof; (3) a "V" type, or reduction thereof; (4) parallel type.

5. The "M" type is found in the Anomalepididae only; it is presumed to consist of components derived solely from the 2nd branchial arches—hypohyals, ceratohyals, and recurrent cornua. Presence of a basihyal element is uncertain.

6. The "Y" type is found in the Typhlopidae and Leptotyphlopidae; it lies in an inverted position, with the median process forward; it is presumed to consist of the basihyal with its lingual process (from 2nd arch), and the 1st ceratobranchials (from the 3rd arch). Either of the parts may be lacking in some species of Typhlops.

7. The "V" type is found in the Uropeltidae, Aniliidae, Xenopeltidae, and Boidae (*sensu stricto*); it lies in an inverted position with the apex of the "V" forward; it is considered to consist solely of the 1st ceratobranchials, derived from the 3rd branchial arches. Union of the cornua is absent in uropeltids, most aniliids, and in some boids; in this reduced condition the cornua are separate, subparallel rods.

8. The parallel type is found in the Colubridae, Elapidae, Hydrophidae, Viperidae, Crotalidae, and in four puzzling boidlike genera

which are, for convenience, grouped into the Boidae (*sensu lato*); these genera are: *Bolyeria*, *Casarea*, *Trachyboa*, and *Tropidophis*. The hyoid is considered to consist of a basihyal and 2nd ceratobranchials; the basihyal may perhaps be absent in some cases. A lingual process is often present.

9. Identification of the parts of each hyoid type is essentially based upon comparison with the basic lizard type. This is not absolutely satisfactory, but at present the embryological evidence is very spotty and inconclusive, and forces the reliance on simple comparison.

10. The hyoid form is quite constant within any given group. Variations are minor and usually represent reduction from the hyoid type. Reduction or even loss of the lingual process and the rest of the basihyal is not uncommon. These variations within any one group are probably not phylogenetically important.

11. The function of the hyoid is, when fixed, to provide a stable attachment for the hyoglossal muscles of the tongue. In many cases it also provides the origin for the retractor of the larynx.

12. Based on the concept of monophyly for the snakes, the earliest stock is conceived of having the basic lizard type of hyoid — basihyal with three pairs of cornua. This is the primitive snake hyoid. At least four lines of evolution can be recognized.

13. One line of evolution produced snakes which lost the 1st and 2nd ceratobranchials. This line produced the modern-day Anomalepididae, with the "M" type hyoid.

14. The remaining stock lost the hypohyals and ceratohyals. Out of this stock came a line which lost the 2nd ceratobranchials but maintained a prominent basihyal and its lingual process. This line produced the modern families Typhlopidae and Leptotyphlopidae, with the "Y" type of hyoid.

15. Another line, or perhaps several lines, diverged from the stock which kept the 1st and 2nd ceratobranchials; these lines produced snakes that lost the 2nd pair of ceratobranchials plus the basihyal — the "V" type hyoid. These snakes are the Uropeltidae, Aniliidae, Xenopeltidae, and Boidae (*sensu stricto*).

16. The final line of evolution involved those snakes which came of the stock that had the 1st and 2nd ceratobranchials plus basihyal, but kept only the 2nd pair plus basihyal — the parallel type hyoid. This line produced the Colubridae, Elapidae, Hydrophidae, Viperidae, Crotalidae, and the four genera *Bolyeria*, *Casarea*, *Trachyboa*, and *Tropidophis*.

17. There have been several obvious trends in the overall evolution of the hyoid in snakes. One has been a loss of two of the three pairs

of cornua found in the basic hyoid form. Another has been a further simplification of the hyoid by loss of the basihyal elements, or the cornua, as apparently happened in some typhlopids. Another trend has been the almost total loss of ossification in any part of the hyoid skeleton; only the typhlopids retain ossification to any degree.

PART II. THE ASSOCIATED MUSCLES OF THE HYOID

A. Preliminary Remarks

The muscles studied closely are those that, with a few exceptions, generally have attachment to the hyoid — in at least some genera if not in all. The exceptions are the *genioglossus*, which does not actually attach to the hyoid but lies very close to the hyoid, and a few others.

Hübner in 1815 published his thesis on the muscular system ("De organis motoris . . .") of a boa. The author has not seen his work, and apparently the only muscles therein that are of concern to this paper are (a) the *latissimus ingluviei* s. *platysma myoides*, which, *fide* Edgeworth (1935), must be equivalent, at least in part, to the *cerato-mandibularis* (as named herein); and (b) the *retrahens laryngis*, or *hyotrachealis*.

In 1827 Anton Dugès gave what seems to be the first fairly complete account of the ventral muscles of the snake head. His plates are quite accurate in what they show, although not complete. Dugès was in error as to the function of certain muscles, believing, for example, that the laryngeal protractor and retractor worked together as a chain to assist in protracting the tongue.

The year 1832 saw the publication of two works of great importance to snake anatomy. Both were by Duvernoy, a careful observer with a clear idea of most of the muscle relationships of the snake head. His

plates are good, and Owen (1866) used them in the first volume of his "On the Anatomy of Vertebrates."

However, probably a more important work than any of the preceding is the 1834 classic by Ernst d'Alton on the python musculature. His plates are excellent and his depiction of the *costocutaneous superior* muscles well done. He used descriptive, generally functional, names for the muscles, but was not always consistent in using the same for text and illustration. Hoffmann (1890), in Bronn's Thierreich, employed d'Alton's work almost en toto, although using many new names.

Other important papers have been by Walter (1887), McKay (1889), Phisalix (1914), Adams (1925), and Lubosch (1933). Lubosch examined a great many species of snakes of various families, unlike most previous investigators who generally studied one, or at most several, species.

The confusing 1937 paper of Gnanamuthu is a lesson in how to complicate the obvious. The papers of Anthony and Serra (1950 and 1955) are incomplete in coverage of the head musculature, although they apparently did not intend to be thorough. Cowan and Hick did a careful piece of work for their 1951 paper, using an unusual approach by comparing cranial musculature in many specimens of the same species, and finding points of constant variation.

Dullemeijer (1956 and 1958) did careful work on vipers in his studies on functional anatomy of the head. Also, Albright and Nelson (1959) presented a clear picture of head muscles in the colubrid *Elaphe*. Sondhi (1958) did a straight anatomical study of *Natrix piscator*, but his paper is confusing and not wholly accurate.

Following a brief, generalized discussion of the associated hyoid muscles in lizards, the snake muscles are treated in groups according to derivation: hypobranchial-spinal muscles and branchial arch muscles.

HYPOBRANCHIAL-SPINAL MUSCLES

This group embraces most muscles of this study. They are derived from myotomic parts of occipital somites and of the anteriormost postcranial somites. Those from the occipital somites are innervated by the hypoglossal nerve, and those from the postcranial somites by spinal nerves. However, there is a very close, natural association between these several somatic masses, and some of the resultant muscles may perhaps be innervated by both the hypoglossal and spinal nerves. The distinction is often not clear.

The tongue is principally a muscular organ and is derived from the occipital somites. Reese (1932) and Sewertzoff (1929) have studied

the tongue development in snakes, the latter in considerable detail. Intrinsic tongue muscles, which will not be considered in this work, are apparently derived from the same mass as the *genioglossi*. The presumptive intrinsic muscles surround the embryonic *hyoglossi*, which will form the bulk of the tongue. The *genioglossi* and *hyoglossi* are both included in this study.

Other hypobranchial-spinal muscles studied are the *geniohyoideus*, *ceratomandibularis*, *neuromandibularis*, *costomandibularis*, *costocutaneus superior*, *sternohyoideus*, *omohyoideus*, and *transversus branchialis*.

BRANCHIAL ARCH MUSCLES

The 1st branchial arches give rise to the jaw muscles, including the intermandibular series of muscles which lie on the ventral surface of the head and interconnect the lower jaws. In many species these are close to the hyoid, and for this reason they are included here.

The 2nd branchial arches give rise to the *constrictor colli* muscles, which are found erratically among snakes, but where present, in most species have some sort of attachment to the hyoid.

The 4th branchial arches give rise to the *hyotrachealis* muscles, the retractors of the larynx. This muscle originates on the hyoid in most snakes.

The synonymy of many of the muscles is extensive and rather varied. The author has tried to select those names which most aptly fit the muscle's origin and insertion; the majority of those selected usually have been traditional. Where a new name was deemed necessary, the same qualifications were used—muscle attachments. It should be noted that the synonymy is not straightforward in many cases, for some muscles described in the literature have been incorrectly illustrated and described. Some have even been divided in such a way that exact correlation of the name in the literature with the one used in this study is not possible.

Examination of specimens has been by gross dissection, usually with the aid of a binocular microscope. The following list of snakes has been examined. A number of other colubrid species were also examined but were not recorded because their musculature showed no particular variations from what was expected.

Anomalepididae: *Helminthophis flavoterminalis*, *Liotyphlops albirostris*.

Typhlopidae: *T. bibroni*, *T. intermedius*, *T. punctatus*, *T. schlegeli brevis*, *T. schlegeli mucroso*.

Leptotyphlopidae: *L. maximus*, *L. septemstriatus*.

Uropeltidae: *Platyplectrurus madurensis*, *Rhinophis blythii*, *Uropeltis ceylanicus*.

Aniliidae: *Anilius scytale*, *Cylindrophis maculatus*, *C. rufus*.

Xenopeltidae: *Xenopeltis unicolor*.

Boidae (sensu lato): *Calabaria reinhardti*, *Charina bottae*, *Constrictor constrictor*, *Eunectes* sp., *Epicrates cenchris*, *Eryx c. colubrinus*, *Liasis childreni*, *Python sebae*, *Sanzinia madagascariensis*, *Trachyboa boulengeri*, *Tropidophis maculatus*, *T. melanurus*.

Colubridae: *Achalinus spinalis*, *Achrochordus javanicus*, *Amblycephalus kuangtunensis*, *Aparallactus lineatus*, *Atretium schistosum*, *Cerberus rhynchops*, *Chersydrus granulatus*, *Dasypeltis scaber*, *Elaphe o. obsoleta*, *Enhydryis enhydryis*, *Fimbrios klossi*, *Haplopeltura boa*, *Heterodon p. platyrhinos*, *Mehelya nyassae*, *Nothopsis rugosus*, *Natrix piscator*, *Sibynomorphus catesbyi*, *Sibynophis collaris*, *Thamnophis elegans vagrans*, *Xenodermus javanicus*, *Xenodon suspectus*.

Elapidae: *Denisonia par*, *Doliophis bilineatus*, *Naja melanoleuca*, *Notechis scutatus*.

Hydrophidae: *Aipysurus eydouxii*, *Hydrophis cyanocinctus*, *Laticauda laticauda*, *Pelamis platurus*.

Viperidae: *Aspis vipera*, *Atractaspis microlepidota*, *Causus resimus*, *Cerastes vipera*, *Echis carinatus*, *Vipera russelli*.

Crotalidae: *Agkistrodon piscivorus leucostomus*, *Bothrops mexicanus*, *Crotalus horridus*.

B. In Lizards

This is merely a brief resume of the associated hyoid muscles found in *Varanus* (Fig. 6), with a comparison of those found in *Anniella* (Fig. 5). For a more complete survey of these muscles in lizards, Richter (1933), Camp (1923), and Oelrich (1956) should be consulted.

Generally speaking, the associated hyoid muscles of lizards are more numerous than in snakes because nearly all lizards have a hyoid with at least two pairs of cornua and some sort of pectoral girdle; these elements provide for more muscles than in snakes where only one pair of cornua and no pectoral girdle are the absolute rules.

In Figure 6 of *Varanus*, the drawings are incomplete: the *costocutaneous superior* and intermandibular muscles are omitted.

HYPOBRANCHIAL-SPINAL GROUP

All the muscles in this group are innervated by the XIIth cranial nerve and/or spinal nerves.

Costocutaneus superior. This muscle lies over the hyoid completely and therefore none of its fibers attaches to the structure.

Ceratomandibularis. This muscle is in two slips. The broad, main slip runs from the middle third of the mandible posteriorly to the anterior edge of the 1st ceratobranchial and also onto the basihyal and its lingual process. A narrow, separate slip lies medial to the main muscle and attaches anteriorly to the dentary a short distance posterior to the tip; it attaches posteriorly to the lingual process. Both slips of the *ceratomandibularis* lie superficial to the hypohyal and ceratohyal.

Neuromandibularis. It arises as a broad aponeurosis over the dorsum of the neck, directly behind the attachment of the *cervicomandibularis*. The *neuromandibularis* then runs anteriorly and ventrally to insert into the mandible on a line with and directly behind the ceratomandibular attachment.

Geniohyoideus. This muscle is in two slips. The larger one arises from the posterior third of the mandible and inserts onto the middle third of the ceratohyal. The smaller slip is slender and arises from the mandible under the anterior portion of the larger slip of the *ceratomandibularis*; it inserts into the free, expanded terminus of the hypohyal.

Ceratohyoideus. This muscle runs between the posterior border of the medial two-thirds of the ceratohyal posteriorly to the anterior border of the 1st ceratobranchial.

Sternohyoideus superficialis. This muscle runs from the sternum anteriorly to a midventral raphe which is continuous onto the basihyal. The muscle overlaps a rear fraction of the *ceratomandibularis*, and has a tendinous intersection.

Sternohyoideus profundus. This muscle runs from the sternum anteriorly to the posterior border of the middle third of the 1st ceratobranchial. This muscle also has a tendinous intersection. The muscle, of course, lies deep to the *sternohyoideus superficialis*.

Omohyoideus. This muscle attaches to the girdle and runs anteriorly and medially to insert upon the rear border of the anterior third of the 1st ceratobranchial. The muscle runs between the two *sternohyoidei*.

Hyoglossus. This is the principal tongue muscle and arises as an encapsulated muscle from the rear half of the 1st ceratobranchial. The two muscles, one on each side, unite at the level of the lingual process to form the bulk of the tongue.

Genioglossus. The *genioglossus* arises from the medial edge of the dentary directly posterior to the tip, and runs as a slender muscle

posteriorly to be attached to the lateral surface of the respective *hyoglossus*.

Geniotrachealis. This muscle arises from the dentary directly behind and partly under the attachment for the *genioglossus*. The *geniotrachealis* then runs posteriorly and medially to insert into the larynx. From this attachment a better name for it might be *geniolaryngeus*, but to be consistent with the name chosen for the homologous muscle in snakes, *geniotrachealis* is the choice.

BRANCHIAL ARCH GROUP

Intermandibulars. These do not attach to the hyoid in lizards, but they are always in the vicinity, and should be mentioned for that reason. The intermandibulars, which are not shown in Figure 6, are wide and their fibers are practically transverse. They are in two sets — an anterior and a posterior. Both arise from the medioventral border of the mandible and attach to the midventral raphe with their mates. The posterior lies between the two slips of the *ceratomandibularis*. These muscles are innervated by branches of the mandibular division of nerve V.

Constrictor colli. This muscle does not attach to the hyoid in lizards; it is always superficial to the rest of the muscles. It forms a broad, aponeurotic band on the ventrum of the throat and is innervated by a branch of nerve VII.

In *Anniella* there are some differences in the musculature from *Varanus*, and these differences are correlated with the reduction in the hyoid skeleton. There is only one pair of cornua — the 1st ceratobranchials. The musculature consists of a *costocutaneus superior*, *ceratomandibularis*, *neuromandibularis*, *sternohyoideus* (a single layer), *hyoglossus*, *genioglossus*, *intermandibularis anterior* and *posterior*, and a *constrictor colli*. Muscles associated in *Varanus* with the hypohyal and ceratohyal — the *geniohyoideus* and *ceratohyoideus* — are missing in *Anniella*.

C. Accounts of Muscles in Snakes

HYPOBRANCHIAL-SPINAL MUSCULATURE

GENIOGLOSSUS

Synonymy. 1827, *Genio-glosse*, Dugès. (*Genio-vaginien*, Dugès. Slip to lingual sheath.) 1832, *Genio-vaginien*, Duvernoy. 1834, *Vor-*

wartszieher des Zungenbeins, d'Alton. 1838, *Genio-glosse*, Meckel. 1839, *Vortzieher des Zungenbeins*, Vogt. 1843, *Genioglossus*, Bendz. 1866, *Genioglossus*, Owen. 1880, *Genio-vaginiens*, Minot. 1887, *Genioglossus*, Walter. 1889, *Genioglossus*, Ludwig Ferdinand v. Bayern. 1889, *Genio-hyo-glossus*, McKay. 1924, *Genio-hyoideus*, DeJong. 1925, *Genioglossus*, Adams. 1929, *Genioglossus profundus* (or *geniovaginalis*), Sewertzoff. 1933, *Geniovaginalis* and *geniohyoideus* (in error?), Lubosch. 1935, *Genioglossus*, Edgeworth. 1937, *Genioglossus* (ventral division, bundle "a" — one slip; dorsal division), Gnanamuthu. 1938, *Genioglossus*, Nishi. 1944, *Genioglossus*, Kesteven. 1951, *Genioglossus*, Cowan and Hick. 1956, *Genio-hyoideus*, Dullemeijer. 1958, *Genio-hyoideus*, Dullemeijer. 1958, *Genioglossus*, Sondhi. 1959, *Genioglossus*, Albright and Nelson.

The pair of *genioglossi* act as protractors of the tongue and are constant in snakes. They are also present in lizards, and the homology is obvious. Each *genioglossus* is a long, slender muscle which may have one or two heads at the origin depending on the species. It is closely applied to the tongue for most of its length.

Origin. For a single head it is usually on the inter-ramal fibrous pad immediately medial to the tip of the dentary bone. If two heads are present the common origin site for the lateral (larger) head is the ventral medial angle of the tip of the dentary. Arising directly lateral to it and closely applied to the external head for part of its length is the *geniotrachealis*. Only in one family, the Typhlopidae (and possibly the Uropeltidae), did the author detect that the lateral head arose from the inter-ramal pad rather than the bone itself, although the connection was close. The medial head, where present, constantly originates on the inter-ramal pad, directly dorsal to the first part of the *inter-mandibularis anterior* (if it is present).

Course. From the origin the fibers proceed medially and posteriorly, soon entering the lingual sheath which invests the intrinsic muscles of the tongue. The medial head, where present, runs almost its complete way along the tongue before uniting with the lateral head.

Insertion. The muscles are bound to the tongue by the sheath, and the fibers do not mingle with the other tongue muscles. The *genioglossi* are now rather lunate or crescentic in transverse section, fitting exactly over the curved lateral faces of the tongue. They extend with the sheath at least as far as the hyoglossal split, but in a few cases they continue past this point, each one, however, still bound to its respective *hyoglossus*; examples of this are found in *Liasis*, *Eryx*, and *Xenopeltis*.

Innervation. The *genioglossus* is served by an anterior branch of the XIIth, or hypoglossal, cranial nerve. The cranial nerves vary in their patterns in snakes; a frequent pattern consists of the IXth plus Xth bound with the XIIth. After IX plus X is given off to the larynx and vicinity, an anterior branch of XII goes on, soon uniting with sensory fibers from V; fibers of XII continue past this point to innervate the *genioglossus* and the *geniotrachealis*.

Action. Simply to protract the tongue. Note that protraction is confined to the part of the tongue anterior to the hyoglossal split — posterior to which the *hyoglossi* usually affix to the hyoid.

Variation. This is slight. Outside of the variation in the number of heads, few differences exist in snakes. In the anomalepidid *Liotyphlops*, the *genioglossus* has two heads and ends at the level of the division of the *hyoglossi* (Fig. 7). In the Typhlopidae the *genioglossi* originate completely from the inter-ramal connective tissue, arising from approximately the same point on the midline just posterior to the tips of the dentary bones. It is probable that these slips represent the medial ones, with the lateral heads not present. The *genioglossi* are fairly wide, each being about one-fifth the width of the tongue, and they end at the level of the hyoglossal division, this being well anterior to the hyoid (Figs. 8 and 9).

In the Leptotyphlopidae each *genioglossus* has a single head, which originates by way of a tendon on the genial surface of the dentary. Muscle fibers arise from this tendon to make up an especially wide and semi-circumferential *genioglossus* (Fig. 10). Together the *genioglossi* completely ensheath the tongue for part of its length. The *genioglossi*, which taper posteriorly, extend to the posterior end of the *hyoglossi* (which attach to the cornua of the hyoid); this condition is found in no other snake.

Rhinophis, a uropeltid, has only the medial head, originating on the inter-ramal pad (Fig. 11). The *genioglossus* ends with the sheath at the hyoglossal split. Another uropeltid, *Platyplectrurus*, on the other hand, lacks the medial head, having only the lateral head.

Other snakes with only a single (lateral) head are the aniliid *Cylindrophis rufus* (Fig. 12, B), the boid *Sanzinia*, the colubrid *Enhydris*, the hydrophid *Aipysurus* (Fig. 17, B), and the crotalid *Bothrops* (Fig. 18, A).

Outside of the Leptotyphlopidae, the presence of the lateral heads alone seems to be of erratic appearance in snakes. That the *genioglossi* have two heads is definitely more common in snakes, and where two heads are present, the medial is always the thinner.

HYOGLOSSUS

Synonymy. 1827, *Hyoglosse*, Dugès. 1832, *Hyo-vaginion*, Duvernoy. 1832, *Cerato-vaginiens*, Duvernoy. 1834, *Zungenbeinzungenmuskel*, d'Alton. 1843, *Ceratoglossus*, Bendz. 1866, *Hyoglossus*, Owen. 1880, *Ceratoglossus*, Minot. 1884, *Hyoglossus*, Ludwig Ferdinand v. Bayern. 1887, *Hyoglossus*, Walter. 1889, *Hyo-glossus*, McKay. 1890, *Hyoglossus*, Hoffmann. 1924, *Hyoglossus*, DeJong. 1925, *Hyoglossus*, Adams. 1929, *Hyoglossus*, Sewertzoff. 1932, *Ceratoglossus*, Reese. 1933, *Hyo-trachealis* (probably in error), Lubosch. 1935, *Hyo-glossus*, Edgeworth. 1937, *Hyoglossus*, Gnanamuthu. 1938, *Hyoglossus*, Nishi. 1941, *Ceratoglossus*, Hershkovitz. 1944, *Thyro-hyoideus* of lacertilians, Kesteven. 1951, *Hyoglossus*, Cowan and Hick. 1956, *Hyoglossus*, Dullemeijer. 1958, *Hyoglossus*, Dullemeijer. 1958, *Hyoglossus*, Sondhi. 1959, *Hyoglossus*, Albright and Nelson.

This muscle is the retractor of the tongue; it also makes up the bulk of this organ. All snakes and lizards have the *hyoglossus*.

Each *hyoglossus* is long, in fact extending the length of what is considered the tongue, and projecting posteriorly from the tongue for a considerable distance as well. Within the tongue itself, the hyoglossal fibers combine with intrinsic muscles; however, the *hyoglossi* tend to keep their identity throughout the actual tongue. The intrinsic muscles, not discussed in this paper, are usually in four sets. They have been described by Minot (1880), Ludwig Ferdinand (1884), and in greater detail by Sewertzoff (1929).

Origin. Without exception the *hyoglossus* originates on some part of the cornu. In the Anomalepididae the muscle originates on the ceratohyal — the exact point of origin being at the ceratohyal-recurrent cartilage junction. Each *hyoglossus* is bound to the cartilage as a unit, and not by individual fibers (Fig. 7).

In the Typhlopidae the fibers attach by small tendons directly to the cornua. This is unique in snakes. The *hyoglossi* utilize the entire anterior surface of the cornua, and there may even be slight encroachment upon the lingual process (Figs. 8 and 9).

In leptotyphlopids, the hyoglossal origin is similar to that found in the remainder of snakes. That is, the posterior end of the muscle is smooth and contained within a connective tissue capsule; no fibers actually attach to the cartilage — instead the encapsulated muscle is bound to it. As a point of difference, however, in leptotyphlopids each *hyoglossus* is bound in its capsule to the entire length of the cornu, the muscle fibers being grossly parallel to the direction of the respective cornu (Fig. 10). In most other snakes the *hyoglossi* are bound to a mere fraction of the cornua.

In these other snakes, where the *hyoglossi* are attached only to a rear fraction of the cornua, the cartilage has a tendency to be somewhat buried in the muscle throughout its length of strong attachment — which is frequently little more than about one-tenth or one-twelfth of the cornual length. Actually, each *hyoglossus* is usually also bound to its cornu for perhaps half the cartilage's length, but this attachment is not strong.

Course. The *hyoglossi* are found in more or less three forms: (1) separate, parallel fibers directly attaching to divergent cornua — Typhlopidae; (2) encapsulated parallel fibers attaching to parallel cornua — families with parallel hyoid type; (3) encapsulated divergent fibers attaching to divergent cornua — "V" hyoid type families and Leptotyphlopidae — and to the ceratohyals in the Anomalepididae.

The *hyoglossi* of group (3) converge anteriorly; this point ordinarily corresponds to the posterior end of the tongue's heavy encapsulating sheath, and therefore to the beginning of the actual tongue itself. In groups (1) and (2), with parallel fibers, the hyoglossal muscles also seem to end at the sheath. In reality the *hyoglossi* in all snakes enter the tongue to make up a considerable part of its musculature, and in all cases the line between the independent part of the *hyoglossi* and the tongue is well demarcated.

Also, in all cases the *hyoglossi* proceed straight anteriorly, keeping their separate identity rather well throughout the tongue. In general the muscles reach the tips.

Insertion. There is no firm insertion, of course. The intrinsic tongue musculature and the surrounding sheath provide a certain amount of attachment.

Innervation. Motor nerves to the *hyoglossi* are from the hypoglossal. At least two branches usually serve each muscle, and occasionally three. The principal branch generally comes off the commonly joined IX + X + XII trunk a short distance anterior to the angle of the jaw, and after several convolutions it penetrates both the sheath and the *genioglossus* immediately anterior to the simultaneous termination of these; then the nerve enters the substance of the *hyoglossus*; the nerve turns and proceeds anteriorly, giving off twigs to the *hyoglossus* and intrinsic muscles. There may also be a branch given off anterior to the main one; if present, it lies anterior to the level of entrance to the tongue of the sensory fibers of the Vth and VIIth. A posterior branch is more common; it is a small twig usually given off the major branch and running to the separate *hyoglossus*. Where the posterior branch is absent, obviously the separate part of the *hyoglossus* must be served by a twig from the principal branch.

Action. The hyoid is stabilized by various muscles acting chiefly in opposition to each other. With their attachment therefore firmly fixed, the *hyoglossi* can contract and thereby shorten the protracted tongue, causing it to retract into its sheath. Also, contraction of some or parts of the hyoglossal fibers included within the tongue must obviously assist various intrinsic muscle actions in causing vibration of the tongue.

Variation. There is little of note. There are length differences which coincide with differences in length of the hyoid (parallel type in particular). The variation in the way the muscles attach to the hyoid, and their divergent or parallel attitude, has already been treated sufficiently.

In hydrophids the tongue, and hence the *hyoglossi*, is relatively short in *Pelamis*, but in several others, at least *Laticauda* and *Aipysurus*, it is relatively long. Fossorial species might be thought of as having weak tongue and hyoglossal development, but such is not necessarily the case. In the typhlopids and leptotyphlopids the *hyoglossi* are very broad and thick, in fact they are relatively by far the bulkiest among snakes (Figs. 8, 9, and 10). A functional correlation with the relatively great bulk is a mystery. The protractors of these tongues, it might be noted, are poorly developed in comparison.

GENIOHYOIDEUS

Synonymy. 1946, *Geniohyoideus*, Warner.

The name is restricted to the muscle found only in the Anomalepididae (Fig. 7).

Presumably the muscle can be homologized with what Richter (1933) named the *geniohyoideus* in lizards, where, in general, this muscle runs between the ceratohyal and the lower jaw and was considered, along with the *cerahyoideus* (*sic*) (also of Richter), as the forward continuation of the *episterno-hyoideus-profundus* (Fig. 6, B).

Origin. In the anomalepidids it originates on the rear half of the lower jaw.

Course. The *geniohyoideus* sweeps posteriorly in a broad sheet that does not meet its opposite anywhere along the midline. It is a thin muscle and almost tendinous medially.

Insertion. It attaches continuously to the hypohyal (transverse bar) and the ceratohyal (descending cornu).

Innervation. Although not demonstrated clearly in the specimens examined, the innervation would surely be by the XIIth.

Action. By counteracting the pull of posthyoid muscles, the *geniohyoideus* would help stabilize the hyoid for the benefit of the hyo-

glossal muscles. It seems unlikely that it would actually pull the hyoid anteriorly, and thereby assist in protracting the tongue.

Remarks. By homologizing this muscle with the one commonly found in the same relative position and with the same general attachments in lizards, there seems to be no problem as to its identity. However, there is also in the anomalepidids examined a slender muscle which anteriorly attaches to the tip of the dentary by a thin tendon and posteriorly attaches to the discernible terminal fraction of the recurrent cornu (Fig. 7). The *geniohyoideus* is in several separate parts in many lizards, and so it seems likely that this slender, independent muscle may well represent another portion of the *geniohyoideus* in anomalepidids. During its course the independent slip lies deep to the principal muscle and therefore is on a different plane; for this reason this slender muscle may be the *ceratomandibularis*, which, because of the loss of the 1st ceratobranchials in the anomalepidids, found a new attachment to the ceratohyal.

In *Typhlops* and *Leptotyphlops* there is a slender muscle attaching anteriorly on the dentary and posteriorly on the lingual process of the basihyal (Figs. 8, 9, and 10). Because the ceratohyals are presumed to be lost in these snakes, this muscle is taken as a *ceratomandibularis*, discussed in a following section. There is always the possibility, though, that this also could be considered a *geniohyoideus*.

The foregoing discussion is, in a way, taking an easy way out by definitely naming the muscle found in anomalepidids. Actually, one must consider the fact that the *geniohyoideus* and *ceratomandibularis* must come from the same premuscular mass, and in relation to the single pair of cornua found in anomalepidids only one ramus-hyoid muscle would be expected to develop from the mass, and this is nearly so. Therefore, it might really be just a convenience to consider the *geniohyoideus* in anomalepidids as a name for the muscular sheet derived from the single premuscular mass. It is always difficult in myology to identify muscles in animals whose ancestors certainly possessed more muscles in the same general area and of the same derivation.

CERATOMANDIBULARIS

Synonymy. 1815, *M. latissimus ingluviei s. platysma myoides*, Hübner. 1827, *Mylo-hyoidien*, Dugès. 1832, *Costomandibulaire* (part), Duvernoy. 1834, *Kieferzungenbeinmuskel*, d'Alton. 1839, *Kieferzungenbeinmuskel*, Henle. 1839, *Kieferzungenbeinmuskel*, Vogt. 1865, *Mylo-hyoidien* (part), Duméril and Jacquot. 1866, *Costomandibularis* (part), Owen. 1887, *Geniohyoideus*, Walter. 1889, *Mylohyoideus*, Ludwig Ferdinand v. Bayern. 1889, *Mylo-hyoides*, McKay. 1890,

Maxillo-hyoideus and *mylo-hyoideus*, Hoffmann. 1900, *Genio-hyoidien* (?), Châine (after Rouvierè). 1906, *Vortwärtszieher des Zungenbeins*, Hager. 1906, *Hyo-maxillaire superficiel*, plus part of *cervico-maxillaire*, Rouvierè. 1914, *Mylo-hyoidien*, Phisalix. 1924, *Mylo-hyoidiens* (?), DeJong. 1925, *Mylohyoideus*, Adams. 1929, *Geniohyoideus* plus *mylo-hyoideus*, Sewertzoff. 1931, *Neuro-costo-mandibularis* (part), Haas. 1933, *Branchiomandibularis spinalis*, Lubosch. 1935, *Geniohyoideus*, Edgeworth. 1937, *Geniohyoideus*, Gnanamuthu. 1938, *Branchioman-dibularis spinalis*, Lubosch. 1944, *Hyomandibular* (?), Kesteven. 1950, *Mylo-hyoidien*, Anthony and Serra. 1951, *Geniohyoideus*, Cowan and Hick. 1955, *Mylo-hyoidien*, Anthony and Serra. 1955, *Geniohyoideus*, Evans. 1956, *Mylohyoideus*, plus parts of *branchiomandibularis* and *neuro-mandibularis*, Dullemeijer. 1958, *Ditto*, Dullemeijer. 1958, *Geniohyoideus* (including possibly part of *genio-lateralis*), Sondhi. 1959, *Neuro-costo-mandibularis, pars hyoidea*, Albright and Nelson. 1962, *Neuro-costo-mandibularis* (part), Kochva.

This muscle is considered to be present, with considerable variation, in all snakes except possibly the anomalepidids. In most snakes it is broad, sheetlike, contributing to the complex known as the *neurocosto-mandibularis*; in a few it is separate and narrow. At a ventral view the broad *ceratomandibularis* in most species covers a considerable portion of the snake head, although the muscle may itself be partially overlain by fibers of the *constrictor colli*, if present, and the *costo-cutaneus superior*.

Innervation is by the XIIth cranial nerve, but since the muscle is so generally integrated in the majority of species with *neuromandibularis* and the *costomandibularis*, which are both served by spinal nerves, it seems appropriate to place the discussion of the *ceratomandibularis* here, followed by the other two.

As can be seen from the synonymy, the name *ceratomandibularis* has not been used in snakes before, so the author has followed Richter (1933) in his work on lizards. Richter called *ceratomandibularis* the muscle which runs from the lower jaw to the 1st ceratobranchial; he considered it an anterior continuation of the superficial layer of the episterno-hyoid complex. In snakes with the parallel type hyoids, the cornua are considered 2nd ceratobranchials and the muscles only have these cornua for attachment. It seems reasonable to homologize this muscle in lizards with the similar one in snakes. Use of the new name for snakes is also strengthened by the fact that a mixed, confusing group of names has been applied to the muscle by previous investigators.

There is a problem as to the proper identity of the muscle in the

typhlopids, leptotyphlopids, and anomalepidids. Possibly the slender muscle either represents the medial slip of the *ceratomandibularis* (as found in lizards), or else it may represent a slip of the deep ramus-hyoid layer, the *geniohyoideus* (also as in lizards). The first possibility is accepted for the typhlopids and leptotyphlopids by reason of attachment to the 1st ceratobranchial, and its similarity to the internal slip in lizards. The first possibility is also suggested, with reservations, for the anomalepidids and has been discussed earlier in the section on the *geniohyoideus*.

Origin. With the exception of the Typhlopidae and Uropeltidae, the origin of the *ceratomandibularis* seems to be largely confined to the dentary in snakes. Usually, then, the line of origin is on the ventral, or at times, slightly lateroventral, surface of the dentary. It extends a variable distance, but most often begins well behind the angle of the dentary, often opposite the middle of the *intermandibularis anterior* muscle or the anterior end of the lingual capsule. The line of origin usually extends posteriorly quite near the end of the dentary, and sometimes onto the compound bone, e.g., *Atretium* and *Epicrates*. The muscle arises from a strong tendinous sheet, often reduced, but in some cases it is large and is closely applied to much of the ventral surface of the dentary. In the Aniliidae the posterior half of the origin of the *ceratomandibularis* is overlain by the tendon of the *neuromandibularis*.

The leptotyphlopids have a narrow *ceratomandibularis* arising from a narrow tendon that is attached to the posterior ventral prominence of the dentary. The tendon lies immediately ventral to the tendon of the *neuromandibularis*.

In the Typhlopidae the very slender tendon, which is very long and extends to the side of the *genioglossus* before giving rise to fibers, attaches to the splenial, although perhaps in some typhlopids where the splenial is much reduced, as *T. braminus*, the attachment must probably be on the angular. The ceratomandibular tendon is separate from the neuromandibular tendon.

In *Rhinophis* the origin of the *ceratomandibularis* is on the compound bone. The narrow tendon is overlaid ventrally by similar tendons of the *neuromandibularis* and *cervicomandibularis*.

Course. From its origin on the lower jaw, the *ceratomandibularis* proceeds posteriorly and somewhat medially. In the typhlopids the muscle is very slender and lies closely applied to the *genioglossus* up to the point where the *ceratomandibularis* angles toward its insertion on the hyoid (Fig. 8). In leptotyphlopids the muscle expands and has

a more or less tripartite form (Fig. 10) discussed more fully under *Insertions*.

The muscle in the uropeltids is narrow and its course is directly toward the hyoid (Fig. 11). In the aniliids the muscle is a sheet and heads for the midline and the hyoid (Fig. 12, B).

The muscle is a broad sheet in the remainder of the serpents and generally runs from the lower jaw toward the midline, the hyoid, and the more or less transverse raphe which is usually shared by the *neuromandibularis* and *costomandibularis*.

Insertion. Some typhlopids have the *ceratomandibularis* inserting on the lingual process. In *T. schlegeli mucroso* the process curves ventrally at its tip and it is upon this curve that the muscle inserts. However, in *T. bibroni* the insertion is along the whole process, and in *T. punctatus* there is a common raphe directly anterior to its insertion upon the process. Also in *T. punctatus*, a slip from the main part of the muscle proceeds posteriorly along the *hyoglossus* to insert by means of a fine tendon to the posterior end of the cornu. In *T. intermedius* the entire muscle inserts upon the cornu by way of a tendon.

Leptotyphlops maximus shows a tripartite division of the *ceratomandibularis* in which the broad first slip inserts upon the midline in a common raphe with its fellow. A second, or middle, slip is more slender and inserts on the lingual process; the third slip inserts over the first several ribs. *L. septemstriatus* is similar.

Rhinophis has a narrow *ceratomandibularis* inserting upon the hyoid. The exact insertion is the lateral edge of about the first eighth of the cornu (there is no basihyal).

Concerning aniliids, in *Cylindrophis maculatus* the *ceratomandibularis* is composed of three distinct slips which attach in different places: a broad medial slip has a long insertion on the median raphe; a lateral one attaches to the anterior fourth of the hyoid cornu; and the middle slip lies over the hyoid on its way to the first several rib ends. *C. rufus* also has a long median insertion on a common raphe. This is followed by fibers attaching to the anterior sixth or so of the cornu. Also, some of the fibers proceed into the area between the cornua to insert commonly on a raphe that also receives fibers of the *costocutaneus superior*. In *Anilius* the insertion is continuous on the median raphe and onto the hyoid, where it involves the lateral edge of nearly half the cornu (Fig. 12, A).

The other snake families possess a type of insertion that is generally common to all — this being an insertion upon an anterior fraction of the hyoid and upon the tendinous inscription in the neurocostomandibular complex, which serves as a common raphe for the three com-

ponents (Fig. 16). One frequent variation is the added presence of the midline insertion upon a raphe common to both ceratomandibulars; this is a sporadic variation, however. For example, it is found in *Xenopeltis*, many colubrids, some hydrophids (*Aipysurus*), some viperids (*Cerastes*), and some crotalids (*Agkistrodon*, *Bothrops*). The boids (*sensu stricto*) seem to lack this raphe; a reason might be that the basihyal is absent in this family.

Insertion upon the hyoid is never more than half the length of the cornu in the xenopeltids and boids (*sensu stricto*), where the cornua are divergent and not proportionately as long as in the parallel type. The length of insertion is seldom more than an eighth of the cornual length in the parallel type.

Fibers of the *ceratomandibularis* usually insert upon the lingual process where one is present. Length of the process does not mean much, however, for *Aipysurus* and *Laticauda* both have a very long process yet the *ceratomandibularis* does not attach to it. *Enhydris*, on the other hand, also has a very long process, and fibers insert upon it as well as the midventral raphe anterior to it. An extreme example is shown by *Atractaspis* where the fibers insert on the median raphe and on the long process alone.

The insertion at the inscription shared with the *neuromandibularis* and *costomandibularis* is extensive. The inscription lies in a more or less transverse plane somewhere near the angle of the jaw, and seems to be composed both of fibrous intermuscular connections and of a thin independent tendon. The inscription in long-preserved specimens may be difficult to find. Cowan and Hick (1951) described two tendinous inscriptions in the garter snake, *Thamnophis*, and maintained that these represent the 1st and 2nd ceratobranchials. It is difficult to differentiate two inscriptions in most snakes, although one is almost always definable. The exact derivation of the inscriptions is, for the moment, obscure.

Achrochordus has a unique *ceratomandibularis* among those snakes with a parallel type hyoid. In this snake the insertion is entirely upon the hyoid, there being no *costomandibularis*, and the *neuromandibularis* is apparently either incorporated into the *costocutaneous superior* or is missing. Of the two parts of the *ceratomandibularis* in *Aipysurus*, the anterior inserts wholly on the lingual process, and the posterior on the cornu. In *Thamnophis* and *Heterodon*, examples among many, posterior fibers of those which are directed for the hyoid may pass ventrally or dorsally to the cornu to insert in a midventral raphe (Fig. 16).

Innervation. The XIIth cranial nerve serves this muscle. Numerous twigs come from the IX + X + XII trunk as well as from the hypo-

glossal branches to the tongue. No twig of the XIIth proceeds posterior to the tendinous inscription where one is found.

Action. The main function is surely to oppose certain other muscles, namely, the *costomandibularis*, *neuromandibularis*, and *costocutaneus superior* (and *omohyoideus*, where present). The opposition must serve to hold the hyoid in a stable position. It has been a common idea that the *ceratomandibularis* muscles must help in protracting the tongue, but observation of snakes during normal tongue protraction, as well as artificial stimulation of the *ceratomandibularis* by electrical means, showed that the hyoid remains relatively stationary during protrusion.

Various secondary functions can be: to assist in elevating the floor of the mouth and to help bring the lower jaws back to a normal position following swallowing of prey.

Variation. The noteworthy variations in the muscle have largely been already given; a brief summary and commentary on them are now made for the sake of convenience.

Presence of the muscle is debatable in anomalepidids. Width of the muscle where it is definitely found ranges from very slender to broad. Slender ones are found in the Typhlopidae, with somewhat broader examples found in the Uropeltidae and Leptotyphlopidae. The other snakes have a generally wide *ceratomandibularis*.

Insertions are always at least partly on the hyoid. Typhlopids, uropeltids, and the strange colubrid, *Achrochordus*, have no other site of insertion. In leptotyphlopids, one slip meets its fellow at a median raphe, another attaches over the rib cage, and the other attaches to the hyoid. *Cylindrophis maculatus* has what appears to be a *costomandibularis* joining the *ceratomandibularis*; neither *C. rufus* nor *Anilius*, however, shows this condition. In the xenopeltids, boids, and remaining families, the *neuromandibularis* and the *costomandibularis* generally effect a union with the *ceratomandibularis*; this broad, extensive complex muscle is termed the *neurocostomandibularis*. The line of junction is marked by a tendinous inscription.

In anomalepidids, typhlopids, leptotyphlopids, uropeltids, and aniliids, the *neuromandibularis* is generally present but does not make connection with the *ceratomandibularis*.

NEUROMANDIBULARIS

Synonymy. 1827, *Cervico-maxillaire*, Dugès. 1832, *Vertebro-mandibulaire*, Duvernoy. 1834, *Nackenzungenbeinmuskel* (part), d'Alton. 1836, *Cervico-mandibulaire* (?), Cuvier. 1839, *Nackenzungenbeinmuskel* (part), Vogt. 1865, Not named but numbered "6," Duméril

and Jacquart. 1866, *Neuromandibularis*, Owen. 1872, *Depressor mandibulae*, Humphry. 1874, *Temporalis* (part), Teutleben. 1889, *Depressor mandibulae*, McKay. 1890, *Cervico-hyoideus*, Hoffmann. 1898, *Neuro-mandibularis*, Kellicott. 1900, *Digastrique* (?), Châine. 1906, *Neuromandibularis*, Hager. 1906, *Cervico-maxillaris* (part), Rouvier. 1914, *Neuro-mandibulaire*, Phisalix. 1925, *Neuro-mandibularis*, Adams. 1929, *Vertebro-mandibular* (?), Fairley. 1929, *Vertebrohyoideus*, Sewertzoff. 1933, *Neuromandibularis*, Lubosch. 1935, *Neuro-costomandibularis* (vertebral head), Edgeworth. 1935, *Neuro-mandibularis*, Radovanović. 1938, *Neuromandibularis*, Lubosch. 1944, *Sterno-hyoid* (?), Kesteven. 1950, *Vertebro-mandibulaire*, Anthony and Serra. 1951, *Neuro-costomandibularis* (neural head), Cowan and Hick. 1955, *Vertebro-mandibulaire*, Anthony and Serra. 1956, *Neuro-mandibularis* (part), Dullemeijer. 1958, *Neuro-mandibularis* (part), Dullemeijer. 1958, *Genio-lateralis*, Sondhi. 1959, *Neuro-costomandibularis*, *pars vertebralis*, Albright and Nelson. 1962, *Neuro-costomandibularis* (part), Kochva.

This muscle is present—with some variation and one exception (*Achrochordus*)—in all snakes. Directly cranial to it, and present in most snakes, is the *cervicomandibularis*. Despite the usual close association of these two muscles, the latter is apparently innervated by the VIIth cranial nerve, whereas the former is innervated by spinal nerves. In the lizards the *neuromandibularis*—or what has been called it anyway—is not universally found. However there is confusion in the literature attending the differentiation of this muscle from the *cervicomandibularis*, and the exact status in lizards is therefore not at all clear. Where the muscle does seem to be clearly represented, for example in *Anniella* (Fig. 5) and *Varanus* (Fig. 6), it is very similar to the muscle in those snakes where the *neuromandibularis* is separate and does not unite, or unites slightly, with the *ceratomandibularis*. But it should be mentioned that in *Anniella* there is at least a partial insertion of the *neuromandibularis* into the *ceratomandibularis*, showing a likely case of parallelism rather than direct homology with the condition in snakes.

Origin. Invariably the muscle arises from an aponeurosis which is attached to the dorsal midline in the nuchal area. The *cervicomandibularis*, where present, always originates in the anterior nuchal region, directly cranial to the *neuromandibularis*.

Course. From the origin the neuromandibular sheet sweeps downward and anteriorly, curving onto the ventral surface. The insertion is a point of variation. The muscle is partially overlaid superficially by the *constrictor colli*, where present, and the *costocutaneus superior*.

Insertion. There are two patterns of insertion. The first is found in the anomalepidids, typhlopids, leptotyphlopids, uropeltids, and aniliids, where the *neuromandibularis* inserts by way of a tendon onto the lower jaw, having no union with the *ceratomandibularis*.

Anomalepidids have a single muscle which seems to be a *neuromandibularis*. It inserts on the dentary.

As an example of the typhlopid condition, in *Typhlops bibroni* (Fig. 8) the fibers attach directly to the articular bone. The muscle lies superficial to the *intermandibularis posterior* and inserts on the bone at the posterior edge of the *intermandibularis anterior*. In *Leptotyphlops* there is a single muscle which is probably the *neuromandibularis*. The insertion is by a long tendon, which lies deep to the *colli* and superficial to the *intermandibularis posterior* and attaches to the same process on the dentary as the *ceratomandibularis*. The tendon of the latter muscle is superficial.

The uropeltid *Rhinophis* has a short tendon which inserts on the compound bone between the tendons of the *ceratomandibularis* and *cervicomandibularis*; the three muscles partially overlap near their insertion. *Platyplectrurus* shows a similar condition. The aniliids all have a more or less separate *neuromandibularis*, with a strong tendon inserting onto the compound bone. The insertion is external to the *ceratomandibularis*; the tendon overlies a small part of the lateral posterior section of the *ceratomandibularis*. The *cervicomandibular* tendon attaches immediately behind the *neuromandibular* tendon. It is noteworthy that in *C. maculatus* the *neuromandibularis* is separate, but in *C. rufus* and *Anilius* fibers from the ribs join the muscle, and these mimic but probably do not represent a *costomandibularis*.

A second kind of insertion pattern is found in the Xenopeltidae, Boidae, and the remaining families: the *neuromandibularis* inserts on the raphe, which is also shared by the *ceratomandibularis* and *costomandibularis*, and in this way the neurocostomandibular complex is formed (Fig. 13). No fibers of the *neuromandibularis* apparently insert on the hyoid itself, although the mixture of fibers sometimes makes this difficult to determine for certain. The raphe is a tendinous inscription that lies roughly transversely about opposite to the end of the lower jaw. In some cases the tendinous inscription is weak and apparently neuromandibular fibers then reach the lower jaw for attachment. This concept is commonly met in the literature, e.g., Sondhi (1958) and Dullemeijer (1956).

Innervation. By twigs of the ventral divisions of several, more anterior spinal nerves.

Action. When the muscle is separate and has no connection with

the *ceratomandibularis* it must have a role in depressing the lower jaw. When the muscle is part of the neurocostomandibular muscle complex the primary action would seem to be in concert with the *costomandibularis* in opposing the action of the ceratomandibular part of the complex muscle and thereby stabilizing the hyoid apparatus. No doubt the neuromandibular part of the complex muscle can also assist the *cervicomandibularis* (and the *depressor mandibulae*) in helping to depress the mandible. Albright and Nelson (1959), with the help of various experimental methods, showed that the *neuromandibularis* is only of value in helping to depress the lower jaw when the jaw has already begun to be depressed; that is, the muscle helps to enlarge the gape.

Variation. A summary can be presented this way: (1) A separate *neuromandibularis* without an accompanying *cervicomandibularis* (Anomalepididae, Leptotyphlopidae); (2) A separate *neuromandibularis* with an accompanying *cervicomandibularis*, but no connection with the *ceratomandibularis* (Typhlopidae, Uropeltidae, Aniliidae); (3) A fairly broad sheet that inserts largely into a tendinous inscription that is also common to the *ceratomandibularis* and to the *costomandibularis*, forming the so-called neurocostomandibular muscle complex (the other families).

Patterns (1) and (2) do not form phylogenetic groups.

With the evolutionary trend toward the incorporation of the three muscles to form the *neurocostomandibularis*, there is a correlated increase in relative width of the *neuromandibularis*. It is slender in the anomalepidids, typhlopids, and leptotyphlopids. In uropeltids and aniliids there is a distinct increase in relative width, particularly anteriorly. In the remaining families the neuromandibular part of the complex is a strong, wide muscle, although still tapering somewhat from the dorsal aponeurosis.

The genus *Achrochordus*, referred to as a colubrid, apparently lacks this muscle, unless its fibers are hopelessly meshed with and indistinguishable from the very extensive *costocutaneus superior*.

COSTOMANDIBULARIS

Synonymy. 1827, *Costo-maxillaire* (part), Dugès. 1832, *Costo-maxillien* (part), Duvernoy. 1832, *Costo-mandibulaire* (part), Duvernoy. 1834, *Nackenzungenbeinmuskel* (part), d'Alton. 1865, *Petit oblique de l'abdomen* (part) (?), Duméril and Jacquart. 1866, *Costomandibularis*, Owen. 1887, *Genio-costalis*, Walter. 1889, *Costo-mandibularis*, McKay. 1890, *Cervico-hyoideus* (part), Hoffmann. 1898, *Submaxillaris* (part), Kellicott. 1906, *Costomandibularis*, Hager. 1914,

Costo-mandibulaire, Phisalix. 1925, *Costo-mandibularis*, Adams. 1929, *Costo-mandibular*, Fairley. 1929, *Costohyoideus*, Sewertzoff. 1933, *Costomandibularis*, Lubosch. 1935, *Neuro-costo-mandibularis* (costal head), Edgeworth. 1935, *Costo-mandibularis*, Radovanović. 1950, *Costo-mandibulaire*, Anthony and Serra. 1951, *Neuro-costo-mandibularis* (costal head), Cowan and Hick. 1955, *Costo-mandibulaire*, Anthony and Serra. 1956, *Branchio-mandibularis* (part), Dullemeijer. 1958, *Branchio-mandibularis* (part), Dullemeijer. 1959, *Neuro-costo-mandibularis*, *pars costalis*, Albright and Nelson. 1962, *Neuro-costo-mandibularis* (part), Kochva.

The *costomandibularis* muscle is not universal in snakes, although it appears to be restricted to them.

In the Anomalepididae, Typhlopidae, and probably in the Leptotyphlopidae, the *costomandibularis* is lacking. A band of fibers in *Leptotyphlops* which is bound to the rib cage and merges with the *ceratomandibularis* probably is only a slip of the latter muscle (Fig. 10). The muscle is present in some form in the remaining families.

This interesting muscle seems to represent specialization of fibers of another muscle and subsequent capture of them by one new site of attachment. From innervation and general relationship it is probable that the *costomandibularis* is composed of a variable number of the altered anterior slips of the *costocutaneous inferior* muscle, whose fibers run from the ventral scales posteriorly to the cartilaginous ends of the ribs (Mosauer, 1937).

In the xenopeltids, boids, colubrids, and poisonous snakes, the *costomandibularis* is a part of the *neurocostomandibularis* complex.

Edgeworth (1935) placed this as true hyoid muscle, that is, one derived from the 2nd branchial arch and thus served by the VIIth cranial nerve. The author could not find any evidence for this position and therefore adheres to the stand that the *costomandibularis* is a derivative of the rectus series of the hypaxial trunk musculature, representing specialized anterior slips of the *costocutaneous inferior*.

Origin. The origin is either directly from a variable number of cartilage ribs (or directly above them on the true ribs), or else upon the rib cage, where the fibers are bound by fascia to the trunk muscles overlying the ribs. The first pattern is the more common. The exact number of ribs providing attachment for slips is often impossible to ascertain, because posteriorly the slips tend to taper off into the *costocutaneous inferior*. Some examples of the ribs involved are: 2-3 in *Tropidophis*, 2-5 in *Thamnophis elegans*, 4-6 in *Atretium*, 6-7 in *Cerastes*. It seems that the 1st rib, which is short, is seldom a site of origin.

In *Thamnophis* there is also a medial slip which arises from the peripheral surface of the lining of the pharyngeal floor.

Course. In the snakes with the parallel type of hyoid, the fibers proceed anteriorly and more or less parallel to and usually lateral to the adjacent cornu. In the snakes with the "V" type of hyoid, the cornua are divergent and the end of each *hyoglossus* and its cornu usually lie superficial to the rib cage so that the *costomandibularis* lies deep to the hyoglossus and cornu; in this case the muscle also lies medial to the posterior part of the cornu. In *Cylindrophis maculatus* the *costomandibularis*, as an exception, lies external to the *hyoglossus*, running forward to insert into the *ceratomandibularis*.

Where the origin of the muscle is upon the rib cage itself, the course of the fibers is lateral to the hyoid, regardless of its type.

Insertion. The principal and usual insertion is upon the common tendinous inscription of the *neurocostomandibularis*. A small medial portion of the *costomandibularis* frequently inserts upon the lateral edge of a cornu as well, directly posterior to the insertion of the *ceratomandibularis*.

The insertion end of the muscle is often covered superficially by part of the *neuromandibularis*; this condition is found in *Xenopeltis*; it is also well marked in *Thamnophis* and to a lesser degree in other species. In *Cerastes* there is no insertion to the hyoid itself, only to the inscription.

In the uropeltids *Rhinophis* and *Uropeltis*, the muscle attaches to the cornu. In *Anilius* the *costomandibularis* does not insert upon the hyoid, but runs deep to the *neuromandibularis* to insert on the compound bone of the lower jaw by a strong tendon shared with the *neuromandibularis*. *Cylindrophis rufus* has slips going to the hyoid and inserting upon the medial edge of the cornu, and may also have a slip inserting on the mandible.

Innervation. By twigs from the ventral division of the spinal nerves, in repetition of those serving the *costocutaneus inferior*.

Action. Primarily to serve as an antagonist to the *ceratomandibularis*; therefore it has a role in the stabilization of the hyoid. Possibly, and certainly in the case of *Anilius* and *Cylindrophis rufus*, the muscle also assists the *neuromandibularis* in depressing the lower jaw.

Variation. A brief summary of the chief variations may be helpful: The muscle is lacking in the Anomalepididae, Typhlopidae, and Leptotyphlopidae—as far as known. In the Uropeltidae the muscle is small and runs from the ribs to the cornu. In the Aniliidae, *Cylindrophis maculatus* has a single muscle, running from the ribs to the

ceratomandibularis; in *C. rufus*, on the other hand, there are presumably two bellies to the muscle, one from the rib ends to the hyoid, and the other from the rib ends to the lower jaw. *Anilius* has only the latter variation.

Most snakes have the origin upon the ends of certain of the anterior ribs and the insertion largely upon the inscription in the *neurocostomandibularis* plus a small bit on the hyoid. In a few there is the condition in which the muscle originates entirely upon the rib cage, bound to the lateral wall muscles; examples are *Xenopeltis* and *Liasis*.

Epicrates has the muscle in two parts: the cranial slip from rib ends 6-8 proceeds lateral to the hyoid to insert in the inscription and on the cornu; the caudal slip, from ribs 8 to at least 10, lies medial to the cornu, inserting on the medial edge of the cartilage, but immediately posterior to the *transversus branchialis*. *Thamnophis elegans* has the interesting condition of a slip originating from the buccal floor between the cornu and the main slip from the ribs.

The genus *Achrochordus* lacks the *costomandibularis*; it also lacks the *neurocostomandibularis*.

COSTOCUTANEUS SUPERIOR

Synonymy. 1827, *Vertebro-hyoidien* (?), Dugès. 1834, *Der grosse, aussere oder Seitenhautmuskel*, d'Alton. 1865, *Peaussier* (continuous with grand oblique), Duméril and Jacquart. 1866, *Squamo-costales*, Owen. 1889, *Obliquus externus*, McKay. 1890, *Cutaneus externus*, Hoffmann. 1904, *Costocutaneus superior*, Buffa. 1916, *Obliquus abdominis superficialis*, Nishi. 1929, *Sternohyoideus* (?), Sewertzoff. 1931, *Hautmuskel* (*H. 2*) (part), Haas. 1932, *Costocutaneus superior*, Wiedemann. 1933, *Cutaneus externus*, Lubosch. 1935, *Cervico-hyoideus* (?), Edgeworth. 1935, *Costocutaneus superior*, Mosauer. 1937, *Sternohyoideus* plus *omohyoideus*, Gnanamuthu. 1938, *Cutaneus externus*, Lubosch. 1946, *Sternohyoideus*, Warner. 1951, *Cervico-hyoideus*, Cowan and Hick. 1956, *Neuro-mandibularis* (part, apparently), Dullemeijer. 1958, *Neuro-mandibularis* (part, apparently), Dullemeijer. 1958, *Omohyoideus* plus *sternohyoideus* plus *sternothyroideus*, Sondhi. 1959, *Costocutaneus superior*, Albright and Nelson.

This is a hypaxial trunk muscle, and also of a repetitious nature, the slips coalescing in a way to form a continuous layer. It is included in this paper because, even though it is a trunk muscle, in the majority of snakes the most anterior slips attach upon part of the hyoid cornua.

The *costocutaneus superior* has been well described for the trunk region (Buffa, 1904; Mosauer, 1935), but due to the difficulty in clearly defining it in relation to the hyoid and "throat" region, its connection

with the hyoid has usually not been shown. However, d'Alton (1834) depicted the muscle in accurate fashion, but after him came a deluge of incomplete illustrations and erroneous ideas as to the nature of the muscles in this region. Dissection, even very careful dissection, on many preserved specimens still leaves the *costocutaneus superior* rather shredded and disarranged in the throat area, and this has apparently been the reason why various authors refer to the *costocutaneus* in the hyoid area as the *sternohyoideus*, or *omohyoideus*, or even *sternothyroideus* (see *Synonymy*). Cowan and Hick (1951) used *cervico-hyoideus*, obviously in following Edgeworth (1935). The author could not decide from the latter's description exactly what muscle is meant, but presumably it must be the hyoid part of the *costocutaneus superior*.

To be sure, the anterior part of the *costocutaneus superior* muscle does lie in a logical place for the *sternohyoideus*, but except in *Typhlops* and *Leptotyphlops* the *sternohyoideus* is probably not present as a recognizable, discrete muscle in snakes. If traces of it do remain in other snakes, they have become so involved in the cutaneous musculature that separation and definition are impossible.

Origin. Because of the presumed function of the anterior group of fibers, their origin can most practically be considered as the anterior ventrals (of varying number according to species) and adjacent rows of lower dorsal scales. For the remainder of the *costocutaneus superior* muscle, the origins are on the ribs, as the name suggests. It should be noted that due to the mixing of the fibers of the anterior group with the muscle as a whole, it is generally impossible to set the limits of the fibers attaching to the hyoid and therefore no exact site of origin can usually be made.

Course. The course of the anterior fibers runs from the origin on the ventral and dorsal scales anteriorly in a slightly curved arc to the hyoid and adjacent tissues; this is true for most snakes. In all snakes the main part of the muscle runs posteroventrally from the ribs toward the lower dorsal scales and the ventrals.

Insertion. It must be mentioned first that in examined *Typhlops* and *Leptotyphlops*, and in *Rhinophis*, *Cylindrophis maculatus*, and *Achrochordus*, the anterior fibers attach to the lower mandibles, thereby completely overlying the hyoid and having no connection to it; in these cases the attachment to the mandibles would likely represent an origin. In *Cylindrophis rufus*, the fibers do not extend to the lower jaws but attach to the posterior edge of the *constrictor colli* muscle; therefore, the *costocutaneus superior* also overlies the hyoid in this species (Fig. 12, B).

In the other examined species, the *costocutaneus superior* inserts upon some part of the hyoid. In the anomalepidids the insertion is upon the posterior or medial edge of the hypohyals and ceratohyals; the recurrent cornua therefore lie deep to the *geniohyoideus* muscle rather than to the *costocutaneus superior* (Fig. 7).

In most cases the fibers inserting on the hyoid do so beginning directly at the anterior end of the cornu (base of the lingual process). Some fibers may begin attaching more posteriorly, as in *Epicrates* (Fig. 14, C), but this is of rare occurrence. The length of insertion on the cornu is seldom but a fraction of the cornual length — ordinarily less than half with the "V" type hyoid, and much less with the parallel type apparatus.

The fibers rarely encroach upon the lingual process, although the crotalids show this tendency, as seen in *Agkistrodon* and *Bothrops* (Fig. 18, A). The latter even has fibers anterior to the process affixing to the midventral raphe.

Posterior to the short length of the insertion on the cornua, the remainder of the hyoid lies deep to the *costocutaneus superior* fibers, so that in the majority of snakes the hyoid is largely covered ventrally by these fibers.

In addition to inserting on some part of the hyoid, the anterior fibers also insert on surrounding tissues, there usually being the *neurocostomandibularis* muscle complex, and the *constrictor colli*.

Innervation. *Costocutaneus superior* fibers are served by twigs from the ventral divisions of anterior spinal nerves. Excepting the first several spinal nerves, each ventral division nerve emerges ventral to the body wall highly convoluted and comes to lie upon the ventral surface of the *obliquus abdominis internus*. Twigs then go to the overlying *costocutaneus*.

Action. A majority of the fibers of the *costocutaneus superior* serve only the trunk and have origins on the ribs and insertions on the scutes and dorsal scales; these fibers draw anteriorly the scales and scutes, which are then secured by the terrain. The *costocutanei inferiores*, which run from the scutes posteriorly to the ribs, act to draw forward the ribs and therefore the snake's body.

The hyoid portion of the *costocutaneus superior* has acquired a different function: assisting in stabilizing the hyoid apparatus so it will be a firm foundation for the *hyoglossi*. When the hyoid part of the muscle contracts, and the scales or scutes which serve as origins are held fast, the hyoid will tend to be drawn posteriorly. This counteracts the anteriorly directed movement initiated by the *ceratomandibularis* muscles and the hyoid is thereupon fixed. The *neuromandibularis* and

costomandibularis, when these are present and inserting on the hyoid plus the neurocostomandibular raphe, have a synergistic action with that of the *costocutaneus superior*.

Naturally in those snakes where the *costocutaneus superior* does not attach to the hyoid and instead merely overlies it, e.g., *Typhlops et al.*, the function of counteracting the *ceratomandibularis* would not occur; the *costocutaneus superior* would then have only an effect on the skin. Its role is taken over by the *sternohyoideus* in the typhlopids and leptotyphlopids, and by the *omohyoideus* in *Rhinophis* and *Cylindrophis maculatus*.

Variation. The major variation involves attachment or nonattachment to the hyoid; this has been discussed previously. There is, however, the case of the colubrid *Achrochordus*, which is given a separate family by some investigators. In *Achrochordus* the *costocutaneus superior* attaches to the lower jaw and is mixed with fibers of the *cervicomandibularis* in a confusing way; the hyoid is quite free from connection with these fibers (Fig. 15, B).

The substantial insertion on the hyoid in *Liotyphlops* is noteworthy; in the other two families of blind snakes the hyoid is missed by the muscle. Warner (1946) designated the fibers *sternohyoideus* in her drawing of *Anomalepis*, but there seems to be no good evidence for giving these fibers that name.

Commonly the *transversus branchialis* sends many of its fibers into the *costocutaneus superior*, and in such cases a clear distinction between the two muscles is impossible.

STERNOHYOIDEUS

Synonymy. 1955, *Sternothyroideus*, Evans.

As a distinct, discrete muscle mass, the *sternohyoideus* can only be indicated as likely in two families: the Typhlopidae (Fig. 8), and the Leptotyphlopidae (Fig. 10). Various applications of the name *sternohyoideus* in other snakes such as by Gnanamuthu (1937), Warner (1946), and Sondhi (1958), are not recognized here. The muscle portions so named by these authors are here considered to represent parts of the *costocutaneus superior* muscle.

The author sees no reason to follow Evans in using the name *sternothyroideus*. There is no true thyroid plate in the larynx of the snake for one thing, and for another the muscle comes nowhere near the larynx.

It would be most reasonable to regard this muscle as the *sternohyoideus*, homologous in lizards to part of the *episternohyoideus* of Richter (1933), and to the sternohyoid of Camp (1923) and Oelrich (1956). In

lizards the sternohyoid muscles have a rather medial placement, with the origin upon the sternum and perhaps part of the clavicle. The muscle in the two snake families where it is considered to be found also has a medial placement, and, because of loss of the girdle, has found a new origin.

Origin. The raphe of the anterior fourth or so of the ventral midline (linea alba). The origin is deep to the abdominal muscles, and the length of attachment is nearly as long as the muscle itself. The fibers arise fanlike before forming the mass of the muscle.

Course. The fibers are directed anteriorly and somewhat deeply. They unite to make up the bulk of the muscle, which gradually expands anteriorly toward the insertion.

Insertion. Upon some part of the hyoid. Most of the insertion is on the entire posterior edge of each cornu; this is true in *Leptotyphlops maximus* and *Typhlops bibroni*. In *T. schlegeli mucroso* there is additional insertion upon the lingual process, and the *sternohyoideus* actually divides closely into three slips on each side; one inserts on the posterior edge of the cornu, one passes ventrally over the cornu to insert along the length of the lingual process, and the third passes deep to the cornu to attach along the lingual process (Fig. 9).

Innervation. A branch of the hypoglossal nerve descends in the mass of the *hyoglossus* to serve the sternohyoid muscle. Very likely, at least the first several spinal nerves also serve it.

Action. Obviously the major function is to stabilize the hyoid apparatus by chiefly counteracting the pull of the *ceratomandibularis*.

Variation. The few variations have been discussed in the several preceding sections. The muscle is very similar in *Typhlops* and *Leptotyphlops*.

OMOHYOIDEUS

Synonymy. 1946, *Omohyoideus*, Warner.

The name is given to a small muscle which runs either from the end of the hyoid or the *hyoglossus* to attach upon the rib cage. It has been found in the Anomalepididae, the genus *Cylindrophis*, the genus *Rhinophis*, and in one examined species of the Boidae, *Eryx c. colubrinus*. The distribution is certainly erratic.

The use of this name for certain muscle fibers in other snakes, as Sondhi (1958) has done for *Natrix piscator*, for example, is ill-advised; these fibers represent *costocutaneous superior* fibers.

In lizards, according to Richter (1933), the *omohyoideus* is part of the *episternohyoideus* complex that unites the first branchial cornua

with the pectoral girdle, and in lizards has, typically, a lateral site of origin on the clavicles and scapula. These bony elements are lost in snakes and if the muscle remains it must seek a new origin. Attachment upon the rib cage has been the solution; this would be somewhat similar in position to the typical lizard origin. Note the posthyoid muscle in *Anniella* (Fig. 5), a limbless lizard, where the reduced pectoral girdle is probably a remnant of the scapula-procoracoid (Stokely, 1947). These muscles in snakes and *Anniella* compare closely in many respects. There are differences, too: in *Anniella* the muscle is relatively much larger, and inserts on the medial edge of the cornu, whereas it always inserts on the lateral edge in snakes.

From its innervation (spinals) and position it is logical to assume that the muscle in snakes, where it is found, is the partial homologue of the *episternohyoideus* complex of lizards and could appropriately be called the *omohyoideus*.

An apparent discrepancy in the Anomalepididae, where the muscle attaches to the ceratohyal rather than to the first ceratobranchial as in lizards and in the few other snakes involved, must be reckoned as the result of the capture of the muscle by the 2nd arch derivative concomitant with the loss of the 3rd.

Origin. The muscle is bound by connective tissue to the lateral body muscles shortly posterior to the end of the cornu. The extent of the origin is variable according to the species.

Course and Insertion. From the origin the muscle runs for a brief distance anteriorly and medially to insert on or about the posterior fraction of the cornu in one of the several following ways: upon the curve formed by the junction of the descending and ascending cornua (Anomalepididae); upon the posterior tip of the *hyoglossus* (*Cylindrophis*); upon the lateral edge of the final third of the cornu (*Rhinophis*); or upon the terminus of the cornu (*Eryx*).

Innervation. By several twigs from the ventral divisions of each of several spinal nerves determined by where the muscle lies in relation to the ribs. The first and second spinals, however, do not seem to be involved.

Action. This is not a large muscle, either in bulk or length. Its purpose is apparently to counteract protraction of the hyoid by the *ceratomandibularis* (or *geniohyoideus* in anomalepidids) and thereby to assist in stabilizing the apparatus. Excepting *Eryx*, it should be noted that, in those snakes having the *omohyoideus*, the *costocutaneous superior* muscle overlies the hyoid and does not consequently attach to it; therefore, in these snakes the *omohyoideus* plays the chief part as an antagonist to the *ceratomandibularis*.

TRANSVERSUS BRANCHIALIS

Synonymy. 1834, *Quermuskel des Zungenbeins*, d'Alton. 1890, *Transversus hyoideus*, Hoffmann. 1910, *Transverse*, Châine. 1935, *Transversus branchialis*, Edgeworth.

This muscle is of varying occurrence, and perhaps may not really be the same muscle for all snakes. Many of the supposed omissions of the muscle are possibly due to the difficulty in separating the *costocutaneus superior* fibers correctly so as to reveal the presence of a distinct layer — the muscle described here. The *transversus branchialis* should be considered unique to snakes.

Albright and Nelson (1959), in their study of *Elaphe obsoleta quadrivittata*, used the name *transversus branchialis* for another muscle, which has a medial attachment to the midline raphe and then splits to have one head attach to the submandibular gland and the other to the oral mucosa.

Origin and Insertion. The two *transversi* arise from a varying length of the medial edges of the cornua, and proceed posteromedially to insert in a midventral raphe, and sometimes also into the *costocutaneus superior* fibers. The *transversus branchialis* fibers always lie at a posteriorly directed angle.

Innervation. The muscle is served by twigs from the ventral divisions of several spinals. This suggests that the muscle is derived from the *rectus cervicis* group.

Edgeworth (1935) thought that the *transversus* is served by the Vth, which places it as a muscle of the first branchial arch. His evidence is wanting, and the author could see no nerve from the mandibular division of the Vth going to the *transversus branchialis* muscle.

Action. Apparently to help retain the form and position of the cartilaginous cornua.

Variation. The families Anomalepididae, Typhlopidae, and Leptotyphlopidae lack the muscle. There is no place for it in these groups because of the relation of the cornua to other muscles.

Rhinophis has a distinct *transversus*, originating on the medial edge of the anterior fourth of the cornu and inserting on the linea alba (Fig. 11).

In the aniliids, *Anilius* has a well-developed *transversus* muscle, attaching to the entire length of the cartilage (Fig. 12, A); in *Cylindrophis rufus*, it attaches to the anterior two-thirds (Fig. 12, B); but in *C. maculatus*, where the hyoid is severely reduced, there is no muscle at all.

Xenopeltis has the fibers originating on approximately the anterior

sixth of each cornu (Fig. 13). Every true boid examined, except *Epirates* and *Python*, possessed the muscle. *Tropidophis* lacks the muscle.

The situation is varied in the remainder of the snakes. Many examined colubrids definitely have it, as *Achrochordus*, *Amblycephalus*, *Thamnophis*, *Nothopsis*, *Fimbrios*, and *Heterodon*. Others do not: *Atracium*, *Haplopeltura*, *Enhydis*, *Cerberus*, and *Sibynophis*. The sea snakes *Aipysurus*, *Laticauda*, and *Hydrophis*, have it, and the elapid *Doliophis* also does. Most other hydrophids and elapids lack it. The viperids *Cerastes* and *Causus* lack the *transversus*. Among crotalids, *Agkistrodon* has the muscle, whereas *Bothrops* does not.

Altogether it appears that except in the anomalepidids, typhlopids, and leptotyphlopids, where it is apparently invariably not developed, the muscle is of erratic appearance within families.

BRANCHIAL ARCH MUSCULATURE

CONSTRUCTOR COLLI

Synonymy. 1832, *Peaucier du cou*, Duvernoy. 1834, *Rückswartszieher des Zungenbeins*, d'Alton. 1839, *Rückswartszieher des Zungenbeins*, Vogt. 1889, *Platysma*, McKay. 1890, *Atlanto-epistropheo-hyoideus*, Hoffmann. 1923, *Constrictor colli*, Camp. 1931, *Hautmuskel (H. 1) (?)*, Haas. 1933, *Sphincter colli (facialis constrictor)*, Lubosch. 1935, *Constrictor colli*, Edgeworth. 1937, *Constrictor colli plus mylohyoideus posterior*, Gnanamuthu. 1938, *Constrictor colli oralis* and *aboralis*, Lubosch. 1944, *Superficial ventral constrictor (C_{sv}. 2)*, or *sphincter colli facialis*, Kesteven. 1951, *Constrictor colli*, Cowan and Hick. 1958, *Mylohyoideus posterior*, Sondhi. 1959, *Constrictor colli*, Albright and Nelson. 1962, *Constrictor colli*, Kochva.

This muscle is of erratic appearance in snakes. The irregularity of its presence is a condition which can even be found within a single genus, e.g., *Python*. The author could find no trace of the muscle in a young *P. sebae* (Fig. 14, A), while Lubosch (1933) plainly illustrated the facial constrictor for *P. molurus*, and even differentiated it into two parts, *oralis* and *aboralis*. Lubosch noted that the muscle is found in an asiatic species of *Tropidonotus (Natrix)*, whereas it is lacking in a European form of the same genus; the two species are presumed to be close relatives. Sondhi (1958) described and illustrated the muscle for the asiatic *Natrix piscator*, naming it the *mylohyoideus posterior*. The author has confirmed the presence of the *constrictor colli* in this species. Lubosch stated that in snakes the *constrictor colli* seems to be in a regressive stage — an observation with which the author concurs.

Dissection has shown that the muscle is often difficult to separate clearly and even to identify. This is particularly true in specimens which have been long or poorly preserved. Because the constrictor lies almost entirely next to the skin and is bound to it rather firmly, skinning of the head and neck can easily disarrange or destroy the muscle so as to make its limits, and even its existence, doubtful. Furthermore, the thinness of the layer contributes to the difficulty in recognizing it.

Origin. Generally by means of a thin aponeurosis from the dorsal area of the posterior part of the head, the nape, or both in combination. Presumably the line of origin should be the dorsal midline, but since the aponeurosis is usually tightly bound to the underlying muscles, this is many times difficult to show.

Usually where the *constrictor colli* is distinctly present, it is broad and covers the angle of the jaw. However, in many boids, e.g., *Epicrates* (Fig. 14, C), *Liasis*, and *Sanzinia*, the muscle is narrow, originating in the area of the nape. The typhlopids have a distinct condition in which the constrictor arises on the lateral aspect of the neck region; the aponeurosis does not reach the dorsal midline.

Course. The *constrictor colli* is either transverse in position from origin to insertion, as in *Typhlops* and *Leptotyphlops*, or else takes on an anteroventral course. In all individuals where it is found, the constrictor forms a sort of half ring about the throat region.

Insertion. Upon part of the hyoid in all but two families — the Typhlopidae and Leptotyphlopidae, where the hyoid apparatus is far posterior to the head, and the *constrictor colli* muscle of each side inserts upon the ventral median raphe. In other snakes the portion of the muscle not inserting on the hyoid either ends in connective tissue over the *ceratmandibularis*, as seen in *Haplopeltura*, or else in a common median raphe. The insertion on the cartilage may be by way of fibers or by an aponeurosis.

Innervation. The VIIth, or facial, nerve serves the *constrictor colli*; the twig comes from the hyomandibular branch which passes over the stapes to innervate the depressor of the lower jaw. The twig to the *constrictor colli* then passes internally to the quadrate, emerges posteriorly, and sends branches to the *cervicomandibularis* as well as to the constrictor.

Action. The contraction of the muscle must, in those where fibers insert into the hyoid, tend to pull back the hyoid in some measure. In this way it could help to counteract the pull of the *ceratmandibularis*. Indeed, d'Alton (1834) called the constrictor "*Rückwartszieher*

des Zungenbeins" (retractor of the hyoid). Still, the main function must be to constrict the pharynx. Of course it cannot be necessary to snakes, for many live without it with obvious success.

Variation. The muscle was found in every family examined except the Uropeltidae. The genera *Rhinophis* and *Platyplectrurus* did not have it, but since the vagaries of the muscle are known it is possible that the muscle is present in some other genus of the family which was not examined.

Typhlopids and leptotyphlopids excepted, the *constrictor colli* has been found wanting in some members of every family. As mentioned previously the absence of it does not seem to be phylogenetically important since close relatives may vary in this respect. Perhaps in the typhlopids and leptotyphlopids, where it seems to be uniformly present, the muscle may represent the primitive condition, for the *constrictor colli* is of constant occurrence in lizards.

Duvernoy (1832a) illustrated the muscle (equals *peaucier du cou*) in the *couleuvre collier* (*Tropidonotus*) as being very broad with the entire insertion upon a common midventral raphe. Inasmuch as in all other examined colubrids, where the muscle is present, the insertion is at least half upon the hyoid, this illustration of Duvernoy's is probably in error. Edgeworth (1933) has used the same drawing.

In the boid genera *Epicrates*, *Liasis*, *Sanzinia*, and *Loxocemus*, the *constrictor colli* is very narrow, and passes in its course behind the angle of the jaw to insert upon the cornu. In these genera it is a distinctive muscle, much narrower than found elsewhere in the snakes.

INTERMANDIBULARS

These muscles lie between the mandibles and are not strictly associated with the hyoid in any species, with one exception. However, they do lie in the immediate vicinity and are readily seen upon any dissection of the hyoid and its musculature. The muscles are not treated here as thoroughly as the others because of their rather incidental importance to the subject. The synonymy is not complete.

The intermandibular muscles are innervated by the mandibular division of the trigeminal nerve. Their general action is to adduct the lower jaws.

There appear to be two sets of intermandibular muscles, but these are divisible in many snakes into several parts or even into several separate muscles. The two basic sets are the: *intermandibularis anterior* and *intermandibularis posterior*. The *intermandibularis posterior* in many species is further separated into the *intermandibularis posterior profundus* and *superficialis*.

The same basic two sets of intermandibulars are recognized in lizards, where the muscles are generally transverse in position and usually very wide (Fig. 5). The *intermandibularis posterior* of lizards is commonly in several slips that interleave with slips of the *ceratmandibularis*.

INTERMANDIBULARIS ANTERIOR

Synonymy. 1832, *Adductor antérieur*, Duvernoy. 1889, *Intermandibularis*, McKay. 1914, *Intermandibulare antérieur*, Phisalix. 1925, *Intermandibularis*, 1 and 2, Adams. 1933, *Intermandibularis*, symphyseal portion, Lubosch. 1935, *Intermandibularis anterior*, Edgeworth. 1951, *Intermandibularis anterior*, Cowan and Hick. 1956, *Intermandibularis anterior* (parts 3 and 4), Dullemeijer. 1959, *Intermandibularis anterior, pars cutaneo-mandibularis*, Albright and Nelson.

This muscle is present in most snakes, but is distinctly missing in *Anilius* and *Xenopeltis*, and is represented only by a tendon in the uropeltid *Rhinophis*. The muscle is generally weakly developed in boids (*sensu lato*), although in *Eryx*, as an exception, the muscle is large; *Trachyboa* and *Tropidophis* the muscle is very slender. In boids and the genus *Cylindrophis*, the lateral attachment is to the medial surface of the tip of the dentary bone. The muscle runs posteriorly and medially to a midline attachment with its mate on the midventral raphe.

The *intermandibularis anterior* is a broad muscle in anomalepidids, typhlopids, and leptotyphlopids; it is particularly transverse in anomalepidids and typhlopids. The muscle may also exist as several distinct masses in typhlopids and leptotyphlopids, and these masses are often at angles to each other (Fig. 10). In anomalepidids, typhlopids, and leptotyphlopids, the anterior muscle, or muscles, usually attach laterally to the medial surface of the dentary but at an appreciable distance posterior to the tip.

The *intermandibularis anterior* is well developed and prominent in the colubrids and poisonous snakes; it is usually in two recognizable but continuous parts (Fig. 17, C). The anteriormost part ("1" of Adams, "part 4" of Dullemeijer) is the larger and thicker one. Its lateral attachment is to the medial surface of the tip of the dentary and its medial attachment is to the fibrous inter-ramal pad. The caudal part ("2" of Adams, "part 3" of Dullemeijer) lies more obliquely and its medial attachment is to its mate at the midventral raphe.

It is obvious that there has been a distinct trend in certain families for a reduction in the *intermandibularis anterior*—Uropeltidae,

Aniliidae, Xenopeltidae, and Boidae (*sensu lato*). For the Colubridae, etc., the trends have been toward a more angular position and subdivision into two continuous but recognizable parts. Particularly in the Anomalepididae and Typhlopidae the basic lizard condition of broad, transverse muscles is still pretty much intact.

INTERMANDIBULARIS POSTERIOR PROFUNDUS

Synonymy. 1890, *Intermaxillaris* (part), Hoffmann. 1914, *Intermandibularis postérieur*, Phisalix. 1925, *Adductor medius*, Adams. 1933, *Intermandibularis*, longitudinal portion, Lubosch. 1935, *Intermandibularis posterior*, Edgeworth. 1951, *Intermandibularis posterior*, pars anterior, Cowan and Hick. 1956, *Intermandibularis posterior*, Dullemeijer. 1959, *Intermandibularis posterior*, pars anterior, Albright and Nelson.

This muscle is found in all snakes examined except the colubrid *Amblycephalus kuanungensis*. It is usually deep to the *ceratomandibularis* and/or *neuromandibularis*, or *geniohyoideus* in anomalepidids. The muscle lies under the neuromandibular tendon and over the ceratomandibular tendon in typhlopids and leptotyphlopids; it lies between the *geniohyoideus* and the slender medial slip of the *geniohyoideus* (*ceratomandibularis*?) in *Liotyphlops*. As an exception to the above rule, in the colubrid *Haplopeltura boa* the *intermandibularis posterior profundus*, if that is indeed the muscle, lies completely superficial to the *ceratomandibularis* (in addition there is another more posteriorly placed superficial intermandibular muscle).

In anomalepidids, typhlopids, and leptotyphlopids, the lateral attachment is to the ventromedial edge of the mandible. This attachment is directly behind or even sometimes overlapping that of the *intermandibularis anterior*. The fibers then run nearly transversely and between the *ceratomandibularis* and *neuromandibularis* (or *geniohyoideus* and slip in anomalepidids) to attach with those of the muscle's mate to the midventral raphe.

In uropeltids, aniliids, boids (*sensu lato*), and xenopeltids, the *intermandibularis posterior profundus* arises from the mandible at a distance from the attachment of the *intermandibularis anterior*. The direction of fibers is anterior and medial and the muscle always lies deep to the *ceratomandibularis*. The medial attachment is to the midventral raphe with its mate; there is at least a slight overlap with the fibers of the anterior muscle, where one is present.

In colubrids and the poisonous snakes, the *intermandibularis posterior profundus* is a stout muscle that attaches to the ventromedial surface of the mandible at about its middle segment. The muscle is

missing in the specimen of *Amblycephalus kuangtungensis* examined. It is very broad in the colubrid *Achrochordus* and attaches to the entire middle third of the mandible. In *Haplopeltura boa* the lateral attachment is over the external adductor muscle of the lower jaw; the fibers are bound to the adductor mass and do not affix to bone. In all species the muscle runs anteriorly and medially to attach to the midventral raphe with its mate. In the hydrophid *Aipysurus* the muscle lies between two slips of the *ceratomandibularis*; this is the only case found of such interleaving among colubrids and poisonous snakes. The *intermandibularis posterior* is either overlapped by or else overlaps the *intermandibularis anterior* at the midventral line in most species. In *Enhydryis*, however, there is a gap between the muscles. In *Haplopeltura* the situation is unique in having both muscles cross at the midline, instead of meeting in a raphe, then interweaving, and continuing on to attach to the opposite mandible just posterior to the attachment of the *intermandibularis anterior*.

In the hydrophid *Aipysurus* a good deal of the medial attachment of the *profundus* is to the very long lingual process of this species. This is the only discovered case among snakes where an intermandibular affixes to the hyoid.

INTERMANDIBULARIS POSTERIOR SUPERFICIALIS

Synonymy. 1889, *Ceratomandibularis*, McKay. 1925, *Adductor posterior*, Adams. 1950, *Intermandibulaire superficial*, Anthony and Serra. 1951, *Intermandibularis posterior, pars posterior*, Cowan and Hick. 1959, *Intermandibularis posterior, pars posterior*, Albright and Nelson.

This muscle is found only in those snakes with a parallel type hyoid, but it is not universally present in them. The muscle, where present, always lies superficial to the *ceratomandibularis*, and it is generally a thin, strongly aponeurotic structure.

Its lateral attachment is to the posterior end of the ventral surface of the compound bone. The muscle is rather slender in most species that have it, although in *Thamnophis elegans vagrans* (Fig. 16, C) it is broad; in *Thamnophis s. sirtalis* (Fig. 16, B) it is narrower. The muscle runs anteriorly and medially and usually steadily expands in width anteriorly. The muscle is deep to the *constrictor colli* if one is present. Those *costocutaneous superior* fibers that attach to the hyoid lie posterior to the *superficialis* and so do not cover it.

The anterior third or so of the *superficialis* is a thin tendon in many species. The medial attachment is always to the midventral raphe with its mate, where there is usually some overlap with the *intermandibularis anterior*; the muscle always is superficial, of course, to the *profundus*.

The muscle has been found in the colubrids *Amblycephalus*, *Atrium*, *Drymobius*, *Elaphe*, *Haplopeltura*, *Heterodon*, *Natrix*, *Pliocercus*, *Thamnophis*, and *Xenodon*, among others; it has been found in the crotalid *Bothrops* and in the viperid *Cerastes*. Examined specimens of *Achrochordus* and *Enhydris*, of the hydrophids *Lapemis* and *Aipysurus*, of the elapids *Denisonia* and *Micrurus latifasciata*, and of the crotalids *Agkistrodon*, *Crotalus*, and *Sistrurus* did not seem to have the muscle. Dullemeijer (1956) did not find one in *Vipera berus*, but McKay (1889) did show one in *Acanthophis*, an elapid. The thinness plus the subcutaneous position of the muscle made dissection and identification of it difficult in many specimens, and this may account for some of the supposed absences of this muscle.

At any rate, there is evidence to show that the *superficialis* is of an inconstant presence in the colubrids; it is mostly absent in the poisonous snakes, and perhaps altogether in the hydrophids.

HYOTRACHEALIS

Synonymy. 1815, *Retrahens laryngis*, Hübner. 1827, *Laryngo-hyoidien*, Dugès. 1834, *Rückwärtszieher des Kehlkopfes*, d'Alton. 1839, *Herabzieher des Kehlkopfes*, Henle. 1880, *Retractor trachea*, Minot. 1886, *Retractor laryngis*, DuBois. 1889, *Hyo-trachealis*, McKay. 1890, *Hyoideo-laryngeus*, Hoffmann. 1898, *Hyo-trachealis*, Kellicott. 1900, *Retractor laryngis*, Göppert. 1929, *Laringohyoideus*, or *retractor trachea*, Sewertzoff. 1933, *Oesophageotrachealis* (probably labeled incorrectly), Lubosch. 1935, *Hyo-laryngeus*, or *hyo-trachealis*, Edgeworth. 1938, *Hyotrachealis*, Nishi. 1944, *Hyo-glossus* (probably in error), or *retractor laryngis*, Kesteven. 1956, *Tracheo-hyoideus*, Dullemeijer. 1958, *Tracheo-hyoideus*, Dullemeijer. 1959, *Hyotrachealis*, Albright and Nelson.

The name *hyotrachealis* is used instead of *hyolaryngeus* because the insertion of the muscle is usually upon what is more properly called the trachea, rather than upon the specialized part of the air tube called the larynx. The distinction, however, is not great.

The muscle is found in all snakes; there were no exceptions uncovered by examination. There are few variations in the position of the insertion and origin. This muscle is apparently unique to snakes.

Origin. In most snakes the site of attachment is upon the respective cornu, but there are exceptions.

The anomalepidids, as shown by *Liotyphlops*, are an exception: fibers of the muscle are bound by connective tissue to the ventral outer surface of the buccal floor lining at a level just anterior to the hypohyals.

The typhlopids are another exception: the origin is upon hypaxial trunk muscles lying over the ends of the rib cage, approximately from ribs 2 to about 4 or 5. The *hyotrachealis* is bound by connective tissue to the muscles.

Leptotyphlopids also are an exception: the origin is again upon the external aspect of the lining of the ventral buccal floor. The level in *L. maximus* is opposite the 1st rib; the site is slightly lateral to the outer edge of the trachea.

Nearly all of the remainder of snakes have the origin upon the cornu, generally upon the lateral edge. In the uropeltid *Rhinophis* the muscle arises at about the anterior fourth of the cornu, but on the medial edge.

As for aniliids, *Cylindrophis maculatus* and *rufus* both have the origin on the lateral edge at about the second fourth of the cornu. In *Anilius* the origin is more posterior.

Xenopeltis has the origin at about one-third the length of the cornu. It usually lies farther posterior in boids, at least to the halfway point or slightly beyond. *Tropidophis* is unusual in having the origin upon the deep face of the raphe of the *neurocostomandibularis*.

In the colubrids and the poisonous snakes, there are a few exceptions to the otherwise straightforward situation. *Heterodon* has the origin upon the muscles of the rib cage; the situation is similar in *Pseudaspis*. *Agkistrodon* is variable: the origin may be either on the rib cage alone or else also the hyoid. Edgeworth (1935) noted that in *Vipera* there is a split origin — one head lies over the rib cage and one attaches to the hyoid. In *Cerastes* the origin is upon the external surface of the ventral buccal floor lining at the level of the end of the *genioglossi*. *Thamnophis* may also show a split origin, one head attaching to the hyoid and the other to the deep face of the *neurocostomandibular* inscription (Fig. 16, C).

Course. The muscle runs from the origin anteriorly to the place of insertion upon the side of the trachea or larynx. In those snakes where the origin is upon the rib cage, or on the buccal floor, and in those with the origin on the hyoid of the "V" type, the course is also somewhat medial. In the parallel type of hyoid, the anterior course of the muscle, when the origin is on the hyoid, is rather straight because the lateral edges of the cornua are about on the same line as the lateral faces of the larynx and trachea.

Insertion. Onto the trachea, or the laryngeal-tracheal region. It is impossible to set a rigid boundary. Variations are minor.

The insertion of the *hyotrachealis* is generally dorsal and anterior

to that of *geniotrachealis* but some genera do have the insertion ventral to the *geniotrachealis* instead, e.g., *Typhlops*, *Amblycephalus*, *Xenopeltis*, and *Agkistrodon piscivorus*. A few snakes show a split insertion, where the hyotracheal fibers attach both dorsal and ventral to the *geniotrachealis*; *Boa cookii* and *Notechis* are examples.

Usually the line of insertion is rather perpendicular, or at most slightly angular, to the tracheal axis. On the other hand, the *geniotrachealis* usually has its insertion along a more or less longitudinal line. Where the hyotracheal insertion is markedly perpendicular, the fibers attach usually to one tracheal ring alone, and sometimes in addition upon the cricoid plate of the larynx.

Action. To withdraw the protracted larynx, plus trachea, into the normal position within the mouth. The *geniotrachealis*, the protractor, is a sturdy, strong muscle, with more bulk than the longer, thinner *hyotrachealis*. Apparently the natural elasticity of the trachea assists the retractor in pulling the protruded larynx back into the mouth.

Innervation. Contrary to Edgeworth (1935), who had the *hyotrachealis* splitting from the hyoglossus and thus acquiring innervation from the XIIth, the cranial nerve involved apparently is the Xth. The vagus nerve basically serves the fourth through sixth arches, from which the laryngeal cartilages and all the intrinsic laryngeal muscles are derived. The *hyotrachealis* would seem to be derived from a mass splitting from the laryngeal intrinsic muscle primordium and growing posteriorly to the site of origin. The *geniotrachealis* develops with the *genioglossus* and thus has *hypoglossal* innervation.

Vogt (1839) had the XIIth serving the muscle. Cowan and Hick (1951) also considered the muscle as a hypobranchial muscle, served by the XIIth; they followed Edgeworth. Göppert, however, in 1910 stated that the IXth serves the muscle; since IX and X at least partially fuse in snakes, his interpretation is understandable.

Actually, in many specimens the dissection does not clearly indicate the nerve. This is because of the plexus-like arrangement of several cranial nerves, to wit, IX, X, and XII. The trunks of these nerves fuse variously, and the branches to various muscles are ascertained with difficulty. Commonly IX plus the superior laryngeal branch of X fuse and run forward together with the fibers of XII (anterior branch); the Xth and the IXth leave to go to the larynx; nerve XII continues forward to the tongue; the XIIth also serves the *genioglossus* and *geniotrachealis*.

Variation. The variations are in the position of the origin or the insertion. The muscle itself is of a rather constant form in snakes.

MISCELLANEOUS MUSCLES

During the course of the dissections, a few other muscles were met with that were not considered germane to the study. Examples of these are the: submandibular gland muscles, *geniotrachealis*, *obliquus abdominis internus*, and *transversus abdominis*. A very short summary of these muscles follows.

There were also a few muscles that were not identifiable. In the anomalepidid *Liotyphlops* there is a muscular sheet between the descending cornu of the ceratohyal and the recurrent cornu. This muscle is not named and it is not shown on Figure 7. The direction of the fibers is anteriorly and medially, and the fibers do not extend the length of either cornu. There are some small muscles in the anterior intermandibular region of typhlopids which are presumably part of the intermandibular series but are not otherwise identified.

Submandibular gland muscles. Along each side of the tongue sheath at the front of the mouth lies a prominent submandibular gland. There are muscles associated with this gland in snakes, and there are at least a pair of them in all species—a “constrictor” of the gland, and presumably a “dilator.” Some typhlopids, at least, have another muscle or two attaching to the gland. The muscles are innervated by nerve V.

In most snakes the *constrictor* attaches to the posterior border or the posterodorsal border of the gland; the fibers in their course lie against the ventral surface of the gland and attach medially to the fibrous inter-ramal pad.

The *dilator* of the gland in most snakes attaches to the posterior apex of the gland; the fibers then run posteriorly and medially, but laterally to the *genioglossus* and *geniotrachealis*, to attach to the midventral raphe. This muscle is called the *transversus branchialis* by Albright and Nelson (1959) after Cowan and Hick (1951); the name does not really seem apt. In typhlopids the muscle is not present, at least recognizably. Instead there is a muscle which runs from the gland laterally to the dentary; it may have the same function.

Geniotrachealis. This is a constant muscle in snakes. It receives a hypoglossal nerve supply. The muscle attaches anteriorly to the apex of the dentary, or to the inter-ramal fibrous pad in some species. In its course it lies on the lateral surface of the *genioglossus*. The posterior attachment is to the trachea, immediately posterior to the larynx. Its action is to protract the larynx and the following part of the trachea.

Obliquus abdominis internus. This muscle is in all snakes and forms a sheet across the ventral aspect of the trunk. Fibers arise on the medial face of the ribs and run anteriorly and medially to attach to the linea alba.

Transversus abdominis. This muscle also arises from the medial face of the ribs, but its fibers run posteriorly and medially to attach to the linea alba. The muscle lies on the deep surface of the *obliquus abdominis internus*.

These two abdominal muscles form a double-layered sheet across the ventral aspect of the trunk. In the Typhlopidae, Leptotyphlopidae, and those snakes with a parallel type hyoid, the muscular sheets lie superficial to the rear fraction of the cornua and its attached *hyoglossi*, etc. In the snakes with a "V" type hyoid, the sheets lie deep to the cornua and attached *hyoglossi*.

D. Discussion

Ventral head muscles considered unique to snakes are the *hyotrachealis*, *transversus branchialis*, *costomandibularis*, and the *neurocostomandibularis*. Only the *hyotrachealis* is universal among serpents.

The *hyotrachealis* muscle, the laryngeal retractor, is of fairly constant form, generally attaching to the hyoid at its posterior end, and always attaching to the side of the trachea, near the larynx; the posterior attachment in some species is to the rib cage or pharyngeal floor. The author could not find a homolog in lizards, either by dissection or noted in the literature. *Varanus* does have a laryngeal protractor, although most lizards do not, but no retractor was revealed in spite of careful search in several species. Watkinson (1916) also recorded no retractor. Apparently the natural elasticity of the trachea is enough to retract it, if the larynx is protracted to any degree in varanids.

The *transversus branchialis* seems to have no homolog in lizards. The muscle unites the two cornua but is of irregular occurrence among serpents. No importance is attached to the variations.

As a muscle considered to be specially formed from slips of the *costocutaneus inferior*, the *costomandibularis* perhaps deserves no separate name, but since this muscle has become well developed and individual, the author feels that it deserves designation. The muscle is not found in all snakes, being absent in anomalepidids, typhlopids, and leptotyphlopids. In the uropeltids the muscle is distinct, although small, and appears to be at its simplest form. The remaining snakes all have the muscle in one form or another; the muscle arises from a variable number of ribs and inserts either (1) to the respective cornu (uropeltids and *Cylindrophis rufus*), (2) to the mandible (*Anilius*), or (3) into the *ceratomandibularis* (*Cylindrophis maculatus*); (4)

most commonly the muscle is a contributor to the *neurocostomandibularis* complex (the remaining snakes with the muscle).

The *neurocostomandibularis* formed by the *costomandibularis*, *ceratomandibularis*, and *neuromandibularis* is unique to snakes, although it is by no means universal, being restricted to the xenopeltids, boids, colubrids, and the poisonous families. Although lizards do not have this muscle, as far as the author is aware, in *Varanus* and *Anniella*, at least, the *neuromandibularis* partially inserts into the *ceratomandibularis*; it might be noted that this combination of the *neuromandibularis* plus *ceratomandibularis* does not exist in snakes. In uropeltids and aniliids, the neuromandibular tendon overlies the origin on the mandible of the *ceratomandibularis*, but no union of the fibers occurs. Lubosch (1933) reported a union for *Cylindrophis rufus*, but in a specimen dissected by the author this was not the case. The *neurocostomandibularis* often has one or more distinct tendinous inscriptions. Ideally all three contributing muscles attach to the inscription, but this is frequently not entirely the case. Many fibers of one of the muscles often proceed past the inscription to attach to the mandible or to the cornu, as the case may be.

The *ceratomandibularis* in lizards is well developed in all species. It is the superficial layer of the ramus-hyoid group (the deep layer is the *geniohyoideus*), and runs from the mandible to the 1st ceratobranchial; occasionally this main, broad sheet is accompanied by a medial, slender one. Among snakes the *ceratomandibularis* is considered absent in the anomalepidids, where the 1st ceratobranchials are lacking; however there is a slender, separate muscle in this family which might possibly be interpreted as being a *ceratomandibularis*. The remaining snakes are considered to have the muscle. In the typhlopids and leptotyphlopids the muscle is very slender and resembles the medial slip of many lizards. In the uropeltids and aniliids, the muscle is relatively broader. In the remainder of the families the *ceratomandibularis* is a broad muscle. Lizards all have a generally broad muscle, and it seems reasonable to suspect that the progenitors of snakes also did. Following this line of thought, the narrow muscles of typhlopids and leptotyphlopids and the moderately broad muscles of uropeltids and aniliids therefore either show reduction in width, or else merely represent the medial slip as seen commonly in lizards. Of course, the *ceratomandibularis* also contributes to the *neurocostomandibularis* complex where it is present. Dullemeijer (1956) felt that the rostral part of the *ceratomandibularis*, as seen in *Vipera*, is really a "mylo-hyoid" muscle, belonging to the intermandibular series.

The *neuromandibularis*, another component of the complex, is pres-

ent in all snakes save *Achrochordus*. It is separate in the anomalepidids, typhlopids, leptotyphlopids, uropeltids, and aniliids; in other snakes the muscle is a major contributor to the *neurocostomandibularis*. In lizards the *neuromandibularis* is commonly present and separate, although some union with the *ceratomandibularis* does take place in *Varanus* and *Anniella*.

The *genioglossus* is generally similar in lizards and snakes. It partially ensheathes the respective *hyoglossus* and affords considerable protractive ability for the tongue. Among snakes, the *genioglossus* is relatively the largest in *Leptotyphlops*. The *genioglossus* in snakes originates on the apex of the dentary bone and/or on the inter-ramal fibrous pad. Genioglossal fibers do not mingle with the intrinsic tongue muscles but are bound to the tongue by a tough sheath. There are no special variations worth noting here.

The *hyoglossus* is similar in both snakes and lizards in several respects: it is long, it is covered anteriorly by a strong membranous sheath, it provides much of the tongue musculature, and it attaches in some way to the hyoid. In lizards the muscles are divergent and encapsulated, affixing to the divergent 1st ceratobranchials. Among snakes the muscles are divergent and encapsulated in the anomalepidids, leptotyphlopids, uropeltids, aniliids, xenopeltids, and boids (*sensu stricto*), and attach to the divergent 1st ceratobranchials, except in the anomalepidids where the divergent muscles attach to the ceratohyals instead. In the colubrids and poisonous families, the 2nd ceratobranchials are parallel, and the attaching *hyoglossi* are encapsulated and juxtaposed. In the typhlopids, the hyoglossal fibers are parallel, but individually affix to the cornua.

The greatest relative development in the bulk of the *hyoglossi* is found in the fossorial typhlopids and leptotyphlopids. In other snakes, the *hyoglossi* are routinely relatively long and slender. The *hyoglossi* of typhlopids and leptotyphlopids do have a great similarity in general appearance and form, but vary, as mentioned previously, in several probably minor ways.

The *geniohyoideus* is commonly found in lizards, where it exists as the deep layer of the ramus-hyoid series, running from the mandible to the ceratohyal. The *geniohyoideus* is considered absent in all snakes except the anomalepidids, where it is a broad muscle extending from the ramus to the hypohyal plus ceratohyal. There is also a slender, separate muscle in anomalepidids which runs from the ramus to the end of the recurrent cornu; this is considered a slip of the *geniohyoideus*, but perhaps it is a slip of the *ceratomandibularis*, otherwise considered lost in anomalepidids. Since the *geniohyoideus* and *cerato-*

mandibularis are derivatives of the same muscle primordium, the attempt at trying to name certain slips is probably not important.

Also commonly found in lizards is the *sternohyoideus*; it frequently is present in several layers. It runs from the sternum to the 1st ceratobranchial. Only in the typhlopids and leptotyphlopids is there anything which can be fairly designated the *sternohyoideus*. In these snakes it is a very well-developed mass, and since there are no sternal elements for posterior attachment the fibers attach posteriorly to the linea alba. The anomalepidids and all other snakes, having lost the 1st ceratobranchials, also have lost the *sternohyoideus*.

The *omohyoideus* is generally a large muscle in lizards, running between the 1st ceratobranchial and the shoulder girdle. The muscle is considered to be present in a few snakes, but this identity is frankly not definite: *Rhinophis*, *Cylindrophis rufus* and *maculatus*, *Eryx*, and possibly *Liotyphlops*. In all cases the origin is over the rib cage and the insertion is on some part of the respective cornu.

A muscle found in all snakes is the *costocutaneus superior*. This muscle is for the most part restricted to the trunk, but the anteriormost fibers do lie on the ventral surface of the head, where they attach in most snakes to the hyoid, although in some species the fibers lie completely over the hyoid to attach to the mandibles. Examples of the latter case are leptotyphlopids, typhlopids, uropeltids, *Cylindrophis*, and the strange colubrid *Achrochordus*. All lizards, apparently, also have these cutaneous muscles, which are derived from the *rectus superficialis* system according to Camp (1923); the fibers, however, never have attachments on the hyoid in lizards.

The *constrictor colli*, where present, partly inserts upon the hyoid in snakes. Indeed, the constrictor may be present or absent in the same species, apparently. With the lizards, the muscle is probably always present and always well developed; it also never seems to attach to the hyoid. The *constrictor colli* is never a sturdy muscle in snakes where it is found, and there has been an obvious trend in evolution for a reduction in the muscle — either entirely or in part.

Intermandibular muscles are present in both snakes and lizards. In lizards, the intermandibulars are generally broad, straplike muscles which often interleave with slips of the *ceratomandibularis*. In typhlopids, leptotyphlopids, and anomalepidids, the intermandibular muscles are broad and rather transverse, reminiscent of lizards. In the other snakes, however, the muscles tend to be more angular in position and relatively more slender. The *intermandibularis anterior* is generally weak or absent in the aniliids, uropeltids, xenopeltids, and boids (*sensu lato*). The colubrids and poisonous snakes have both the *inter-*

mandibularis anterior and *intermandibularis posterior profundus* well developed. The *intermandibularis posterior superficialis* has been found in many colubrids and has also been found in a viperid and a crotalid; many colubrids and most poisonous snakes seem to lack the *superficialis*.

E. Summary

1. Associated hyoid muscles of the lizard *Varanus* are the: *costocutaneus superior*, *hyoglossus*, *genioglossus*, *ceratomandibularis*, *neuromandibularis*, *geniohyoideus*, *sternohyoideus*, *omohyoideus*, *ceratohyoideus*, *intermandibularis anterior* and *posterior*, and *constrictor colli*.

2. Associated hyoid muscles of the snakes are the: *costocutaneus superior*, *hyoglossus*, *genioglossus*, *ceratomandibularis*, *costomandibularis*, *neuromandibularis*, *neurocostomandibularis*, *geniohyoideus*, *sternohyoideus*, *omohyoideus*, *transversus branchialis*, *hyotrachealis*, *intermandibularis anterior*, *intermandibularis posterior*, and *constrictor colli*. No one species has them all.

3. Muscles unique to snakes, but not found in all species, are the: *costomandibularis*, *neurocostomandibularis* complex, *transversus branchialis*, and *hyotrachealis*. The *hyotrachealis* is the single unique muscle common to all snakes.

4. The hypobranchial-spinal group of muscles are innervated by the hypoglossal nerve and spinal nerves and include all the muscles of No. 2 except the *hyotrachealis*, *intermandibulars*, and *constrictor colli*.

5. Anterior fibers of the *costocutaneus superior* attach to the hyoid in most snakes. However, these fibers attach only to the lower jaws in typhlopids, leptotyphlopids, uropeltids, and the aniliid *Cylindrophis*.

6. Hyoglossal fibers are parallel in typhlopids, and attach directly to the cornua. The *hyoglossi* are divergent and encapsulated in anomalepidids, leptotyphlopids, uropeltids, aniliids, xenopeltids, boids (*sensu stricto*), and lizards. The remaining snakes have the *hyoglossi* parallel and encapsulated.

7. The *genioglossi* are similar for all snakes; they actually insert into the tongue, having no attachment to the hyoid.

8. The *ceratomandibularis* is found in all snakes save the anomalepidids, perhaps. It runs between the mandible and the cornu, and is also a part of the *neurocostomandibularis* where present. The *ceratomandibularis* is narrow in typhlopids, leptotyphlopids, uropeltids, and aniliids.

9. The *costomandibularis* is considered to be formed of modified slips of the *costocutaneus inferior*. It is not found in typhlopids, leptotyphlopids, and anomalepidids.

10. The *neuromandibularis* is found in all snakes, with a possible exception of *Achrochordus*. It runs between the dorsum of the neck and the mandible or the neurocostomandibular inscription.

11. The *neurocostomandibularis* is a large muscle complex which is composed of the *ceratomandibularis*, *costomandibularis*, and *neuromandibularis*, in xenopeltids, boids, colubrids, and poisonous snakes. There is usually a common tendinous inscription.

12. The *geniohyoideus* is found only in the anomalepidids; it runs from the mandible to the hypohyal and ceratohyal.

13. The *sternohyoideus* is found only in the typhlopids and leptotyphlopids, where it is very large; it runs from the hyoid posteriorly to the linea alba.

14. A small muscle reservedly called the *omohyoideus* is found in a few snakes of several families. It runs from the rib cage to the cornu.

15. The *transversus branchialis* connects the two cornua; it is of erratic distribution in snakes.

16. The *hyotrachealis* attaches to the trachea and to the cornu in most snakes; in a few it attaches posteriorly to other neighboring tissues. It is innervated by X.

17. The intermandibulars are innervated by V. The anterior set is absent or weak in many families; the *posterior profundus* is always present and strong; the *posterior superficialis* is found in many colubrids and some poisonous snakes.

18. The *constrictor colli* is innervated by VII. It is of erratic appearance in snakes; where present it partly attaches to the hyoid in many snakes.

19. Miscellaneous muscles in the vicinity are the submandibular gland muscles, *geniotrachealis*, *obliquus abdominis internus*, and *abdominis transversus*.

PART III. PHYLOGENETIC SIGNIFICANCE OF THE HYOID AND ITS ASSOCIATED MUSCLES IN SNAKES

A. Discussion

Brief summaries of the hyoid structure and associated muscles of the lizard *Varanus* and the families of snakes follow.

1. *Varanus*: Hyoid — complete basihyal, hypohyals, ceratohyals, plus 1st ceratobranchials (bony). *Costocutaneus superior* does not attach to hyoid. *Hyoglossi* divergent, attach to ceratobranchials. *Ceratomandibularis* large, in two slips. *Neuromandibularis*. *Geniohyoideus* in two slips. *Ceratohyoideus*. *Sternohyoideus* in two layers, *superficialis* and *profundus*. *Omohyoideus*. *Intermandibularis anterior* and *posterior*; broad and transverse.

2. Anomalepididae: Hyoid — basihyal?, hypohyals, ceratohyals with recurrent cornua; no lingual process; "M" type. *Costocutaneus superior* attaches to hyoid. *Hyoglossi* divergent, encapsulated, attach to ceratohyals. *Ceratomandibularis* probably not present. *Geniohyoideus* present, between mandible and hyoid. *Sternohyoideus* missing. *Omohyoideus*? small. *Intermandibularis anterior* and *posterior*; broad and transverse.

3. Typhlopidae: Hyoid — complete basihyal plus 1st ceratobranchials; some parts may be missing in some species; "Y" type; may be bony. *Costocutaneus superior* does not attach to hyoid, only to jaws. *Hyoglossi* large; parallel fibers attach to hyoid directly. *Ceratomandib-*

ularis very slender. *Neuromandibularis* separate. *Sternohyoideus* large, attaches to linea alba. *Intermandibularis anterior* and *posterior*; broad and transverse.

4. Leptotyphlopidae: Hyoid — like in Typhlopidae, but never reduced and never bony. *Costocutaneus superior* does not attach to hyoid, only to jaws. *Hyoglossi* large; divergent muscles encapsulated. *Genioglossi* greatly expanded to cover tongue sheath. *Ceratomandibularis* very slender. *Neuromandibularis* separate. *Sternohyoideus* large, attaches to linea alba. *Intermandibularis anterior* and *posterior*; broad and transverse.

5. Uropeltidae: Hyoid — 1st ceratobranchials only; cornua separate; "V" type. *Costocutaneus superior* does not attach to hyoid. *Hyoglossi* divergent. *Ceratomandibularis* narrow and separate. *Neuromandibularis* separate. *Costomandibularis* present and separate, attaches to hyoid. *Omohyoideus*? *Intermandibularis posterior profundus* only.

6. Aniliidae: Hyoid — 1st ceratobranchials only; cornua joined or separate; "V" type. *Hyoglossi* divergent. *Ceratomandibularis* rather broad, separate. *Neuromandibularis* separate. ANILIUS — Cornua united anteriorly. *Costocutaneus superior* attaches to hyoid. *Costomandibularis* attaches to mandible. *Intermandibularis posterior profundus* only. CYLINDROPHIS — Hyoid reduced; cornua not joined anteriorly. *Costocutaneus superior* does not attach to hyoid. *Costomandibularis* attaches to hyoid (*rufus*), or to *ceratomandibularis* (*maculatus*). *Omohyoideus*? *Intermandibularis anterior* weak; *intermandibularis posterior profundus* well developed.

7. Xenopeltidae: Hyoid — 1st ceratobranchials only; joined anteriorly; "V" type. *Costocutaneus superior* attaches to hyoid. *Hyoglossi* divergent. *Neurocostomandibularis*. *Intermandibularis posterior profundus* only.

8. Boidae (*sensu stricto*): Hyoid — 1st ceratobranchials; cornua joined or separated; "V" type. *Costocutaneus superior* attaches to hyoid. *Hyoglossi* divergent. *Neurocostomandibularis*. *Intermandibularis anterior* usually weak; *intermandibularis posterior profundus* well developed.

9. Colubridae, Elapidae, Hydrophiidae, Viperidae, and Crotalidae: Hyoid — basihyal plus 2nd ceratobranchials; lingual process and possibly complete basihyal sometimes missing; parallel type. *Costocutaneus superior* attaches to hyoid. *Hyoglossi* parallel and juxtaposed. *Neurocostomandibularis*. *Intermandibularis anterior* and *intermandibularis posterior profundus* both well developed; an *intermandibularis posterior superficialis* in addition in some species, particularly in the Colubridae.

10. *Trachyboa*, *Tropidophis*, and possibly *Bolyeria* and *Casarea*: Same as No. 9, except they have a very weak *intermandibularis anterior*, and the *intermandibularis posterior profundus* only.

11. *Achrochordus* (a colubrid genus with many strange features): *Costocutaneus superior* does not attach to hyoid. *Neurocostomandibularis* absent; *ceratomandibularis* is separate; apparently no *neuro-mandibularis* or *costomandibularis*.

At this point it is a temptation to suggest a set of superfamilies. Smith and Warner (1948) prepared such a provisional classification based on the four types of hyoid form: Anomalepoidea, Typhlopoidea, Boidoidea, and Colubroidea. At first glance this seems like a very efficient and reasonable classification, but when the associated hyoid musculature is taken into account, it is not entirely satisfactory. Rather than prepare another provisional set of superfamilies, the author chooses to discuss the possible lines of evolution of snakes as suggested by the hyoids plus their associated muscles. No special names are proposed for these lines.

First, it seems worthwhile to try to interpolate the hyoid anatomy of both snakes and lizards, in order to come up with some sort of likely primitive snake condition. Once having that, the evolutionary lines can be followed more easily.

From such interpolation, a possible ancestral stock of the snakes might have had the following anatomy: (a) Hyoid—derived from arches 2, 3, and 4; complete basihyal, hypohyals, ceratohyals, 1st ceratobranchials (bony), and 2nd ceratobranchials. (b) *Costocutaneus superior* fibers attach to jaws, not to hyoid. (c) *Hyoglossi* divergent, attaching to 1st ceratobranchials. (d) *Genioglossus* attaches to tip of dentary. (e) Two ramus-hyoid muscles: a deep *geniohyoideus*, attaching to hypohyal and ceratohyal; a superficial *ceratomandibularis*, attaching to 1st ceratobranchial. (f) Two hyoid-pectoral girdle muscles: *sternohyoideus* and *omohyoideus*. (g) *Neuromandibularis* separate, attaching to mandible. (h) *Geniotrachealis* present. (i) *Hyotrachealis* attaches to buccal lining posteriorly. (j) *Intermandibularis anterior* and *posterior*; broad and transverse. (k) *Constrictor colli* present, probably not attaching to hyoid.

From this stock, possible evolutionary lines can be worked out with the evidence offered by the hyoid and its musculature (Fig. 19).

(1) The first line gave rise to the modern anomalepidids; these changes were made from the primitive stock: (a) Loss of 1st and 2nd ceratobranchials, and probably the entire basihyal. (b) *Costocutaneus superior* fibers affixed to hyoid. (c) *Hyoglossi* made new attachments to the ceratohyals. (d) *Sternohyoideus* lost. (e) *Ceratomandibularis*

apparently lost; there is a slip, separate from the *geniohyoideus*, which might represent the *ceratomandibularis*.

The significant loss in the number of muscles and parts of the hyoid from the primitive stock seems to indicate that much time passed in the evolution of the anomalepidid snakes as we see them today. The unique presence of the presumed *geniohyoideus* and of a hyoid composed only of 2nd arch derivatives surely indicates that this group is far removed from other snakes, and that its evolution has been along a line that diverged early from the primitive snakes.

It is probable that among the forms evolving in the main group of the primitive stock were those which lost the hypohyals and ceratohyals, and the *geniohyoideus*. It was these snakes which seemed to have become the main stock. From this stock emerged a second line.

(2) This line later split to give rise to the modern typhlopids and leptotyphlopids; to give rise to the line, these changes were made from the primitive stock: (a) Loss of 2nd ceratobranchials. (b) *Hyoglossi*, and tongue in general, relatively enlarged. (c) *Ceratomandibularis* reduced to a slender muscle. (d) *Omohyoideus* lost.

The typhlopids and leptotyphlopids have not often been considered closely related, principally because of differences in the skulls. In fact they have not usually been considered as even having a common ancestral line. However, evidence presented here is contrary to at least the latter view. The hyoid of the two families is similar in composition, and it is morphologically unlike those of other snakes. It is true that the "V" type cornua are also 1st ceratobranchials, but the lingual process, which is so distinct and usual in the "Y" type, is missing in the "V" type.

Typhlopids and leptotyphlopids have relatively large hyoglossal muscles, totally different in general form from other snakes. The two families both have a very slender, independent *ceratomandibularis*, which is unlike that of other snakes. The relatively large, almost massive, *sternohyoideus* is unknown for other snakes. These are surely enough pieces of evidence from the ventral head region to give rise to a distinct suspicion that these snakes have had a similar ancestry, which was, itself, on a line removed from the other snakes.

After the emergence of the second line, the main stock had forms with this anatomy: the *sternohyoideus* is lost, the intermandibulars become angular in position, and the *hyotrachealis* takes attachment to a cornu; then a new muscle, the *costomandibularis*, forms from the *costocutaneus inferior*. These snakes made up a new or continuing stock from which emerged a third line.

(3) This line evolved into the modern uropeltids; these changes were

made from the stock: (a) Loss of 2nd ceratobranchials and basihyal. (b) *Intermandibularis anterior* reduced appreciably. The status of the uropeltids as a family is by no means clear. There are about six genera usually recognized as belonging in this family. It may well be that at least some of these will be found to be more naturally allied with the aniliids.

Another small line, the fourth, also diverged from this stock.

(4) This line gave rise to the aniliids; these changes were made from the stock: (a) Loss of 2nd ceratobranchials and basihyal. (b) *Ceratomandibularis* broadened. (c) *Intermandibularis anterior* reduced.

The relationships of this group as a natural family are also questioned. The aniliidae is usually formed of three genera. Two are South Asiatic — *Anomalochilus* (not seen) and *Cylindrophis* — and one is South American — *Anilius*. *Cylindrophis* differs from *Anilius* in several outstanding ways, indicating at least a subfamily division. *Cylindrophis* has an edentate premaxilla, a coronoid bone, a divided anal, and scale pits. *Anilius* shows the opposite condition for each of these traits.

In any case the aniliids probably have a close alliance with the uropeltids, and this seems borne out by comparing the generally similar hyoid anatomy of the two families.

A major anatomical and evolutionary event then occurred in the stock by the formation of the *neurocostomandibularis*, a composite muscle which was made up of the *ceratomandibularis*, *costomandibularis*, and *neuromandibularis*. The remainder of the snakes, with the exception of *Achrochordus*, all have this distinct composite muscle.

The stock is now considered to have consisted of snakes with a hyoid composed of a basihyal, 1st and 2nd ceratobranchials, and with a *neurocostomandibularis*, as well as *costocutaneus superior*, *constrictor colli*, intermandibulars, etc. This stock is also considered to have been the fifth line of evolution.

(5) This line, or stock, gave rise to the xenopeltids and the boids (*sensu lato*); there was a general reduction in the *intermandibularis anterior*.

Then, one line came off this stock which retained the 2nd ceratobranchials but lost the 1st pair; these snakes became the genera *Trachyboa*, *Tropidophis*, *Bolyeria*, and *Casarea*. The *hyoglossi* became juxtaposed and attached to the cornua.

The rest of the stock lost the 2nd ceratobranchials and the basihyal; this line further split to give rise to the boids (*sensu stricto*) and the xenopeltids. In the xenopeltids the *intermandibularis anterior* was totally lost.

Frankly, the position of the four genera named above is once again noted as uncertain and puzzling. These snakes seem boidlike in most characteristics, and certainly have the general habitus of boas. Yet their remarkable possession of a parallel type hyoid cannot be easily discounted. *Trachyboa* and *Tropidophis* lack a coronoid bone in the mandible, whereas Anthony and Guibé (1952) reported that *Bolyeria* and *Casarea* have a coronoid, as the greater number of the true boids do. Anthony and Guibé proposed the subfamily Bolyerinae, under Boidae, for these two genera. This brief discussion of these four genera merely points up the fact that the anatomical information about them is incomplete.

The genus *Xenopeltis* has long been assigned its own monogeneric family, chiefly for the reason of its having a peculiar lower jaw — there being an intercalated coronoid bone and a movable dentary. There has been a view toward grouping this species with *Loxocemus*, a neotropical genus sometimes recognized as the only new world python (Haas, 1955). The two snakes differ in lower jaws — *Loxocemus* being boidlike — but have certain other things in common: premaxillary teeth present, two functional lungs, free projecting tabular bones. Haas disclosed that the two also have similarities in cranial musculature involving the *adductor externus*, and a double *depressor mandibulae*. He decided that *Loxocemus* should be regarded as having split off from the stock where the Xenopeltidae and the Boidae have diverged. The anatomy of the hyoid may not be particularly significant as regards the *Xenopeltis-Loxocemus* relationship. *Xenopeltis* lacks the *intermandibularis anterior*, but otherwise, like *Loxocemus*, has a true boid type of musculature associated with the hyoid.

It appears to the author that the snakes with the "V" type hyoid, plus *Trachyboa*, etc., are the ones which present the greatest number of problems in defining families and familial relationships.

From the stock of the fifth line, another line diverged which became very important and produced the majority of snakes; this was the sixth line.

(6) This line gave rise to the colubrids, elapids, hydrophids, viperids, and crotalids; these changes were made from the stock: (a) Loss of 1st ceratobranchials. (b) *Hyoglossi* became juxtaposed and attached to 2nd ceratobranchials. (c) *Intermandibularis posterior superficialis* added for some species. (d) *Intermandibularis anterior* enlarged.

The apparently aberrant genus *Achrochordus* has a strange and unique set of muscles: the *neuromandibularis* and *costomandibularis* have been lost, the *intermandibularis posterior profundus* is extremely broad, and the *costocutaneus superior* fibers attach to the mandibles

and therefore overlay the hyoid. This genus surely represents a case of losses and modifications of muscles.

The five families included as being derived from the sixth line have a great deal in common, and obviously stand independently of the rest of the snakes — with the possible exception of the genera *Trachyboa*, etc. The five families have been variously interpreted by many authors, so that it is easy to find in the literature different familial classifications. For example, a number of genera lumped together into the Colubridae here have often been separated into their own families, such as the Achrochordidae, Amblycephalidae, Dasypeltidae, etc. The Elapidae, Hydrophidae, Viperidae, and Crotalidae also have been considered conservatively herein.

Some authors, e.g., Dowling (1959), have made the hydrophids a subfamily, Hydrophinae, in the Elapidae, and the pit vipers a subfamily, Crotalinae, in the Viperidae.

In examining the preceding phylogenetic patterns it becomes obvious that reductions and losses have largely characterized the evolutionary history of the hyoid and its associated muscles in snakes. Furthermore, it is herein considered that some of the reductions and losses of the same muscles or parts of the hyoid occurred in different lines, and therefore more than once in the phylogenetic scheme (parallelism or convergence). For example, it seems likely that loss of the 4th branchial arch components — 2nd ceratobranchials — occurred in the line that gave rise to the typhlopids and leptotyphlopids, also in the small lines that gave rise, respectively, to the uropeltids and aniliids, and in the line of the stock which gave rise to the true boids and xenopeltids. There are other examples among the musculature.

The *costomandibularis* is the single new muscle that appeared, and it really is a modification of another muscle — the *costocutaneus inferior* — that was already present. The *neurocostomandibularis* was formed as an amalgamation of three muscles already there but separate. Another noteworthy modification was the shift in the posterior attachment of the *hyotrachealis* from the buccal mucosa to the available cornu.

The phylogenetic tree proposed, and shown diagrammatically in Figure 19, is of course based on the hyoid and its musculature. By altering the emphasis on hyoid form and the muscles, it would be easy to come up with another diagram that differed in some parts if probably not in all. For example, it might be considered that the divergence of the lines of snakes with the parallel type hyoid occurred much earlier from the stock than is shown on the plate. The formation of the *neurocostomandibularis*, which occurs in the parallel type as

well as in many of the snakes with the "V" type hyoid, would then be considered a matter of convergence.

Comparison of the diagrammatic tree illustrated in Figure 19 with several in the literature does not show many differences. Mahendra (1938) based his diagram mainly on osteological characters, and his diagram is not remarkably different from the author's. He did not recognize the Anomalepididae, and he considered Leptotyphlopidae and Typhlopidae as unrelated families coming off a stock in quite separate directions; these are the outstanding exceptions to the author's diagram. Schmidt's (1950) diagram is much like Mahendra's, although he recognized the Achrochordidae as a separate family.

Bellairs and Underwood (1951) summarized the anatomy of snakes and its phylogenetic importance. They also prepared a phylogenetic diagram, which differs in some respects from the one shown in Figure 19. For one thing, they included the anomalepidids with the typhlopids. Dowling (1959) in his review of the studies on the relationships of snakes prepared a diagram on the bases of adaptiveness to habitat and of morphological characters. His diagram differs in some ways from the author's: he did not recognize the anomalepidids, and he supported the view that the boids are the primitive and generalized snakes, with the other snakes having radiated away from them.

Because so much, if not all, of the phylogenetic study of snakes must depend upon interpreting the modern species alone, the past history will always be one of debate and conjecture. For example, in Dowling's work he uses the boids as primitive snakes, but there seems to be no good reason why modern boids should be a great deal like the actual primitive stock. The modern species must surely be thought of as having changed from earlier forms, and in this way are not the truly primitive animals that he, and others, have made them out to be. Indeed, as far as the hyoid and its musculature are concerned, the modern-day boids, either in the restricted or in the broad sense, show no more proof of being what the primitive snakes must have been like than other snakes.

As far as the phylogeny of snakes goes, the truth is that the number of snake families, or natural groups, is obviously rather small, no matter how one interprets the classification. About twelve families conservatively, and perhaps fifteen liberally, are about all that one has to work with. Certainly the reasonable ways in which the phylogenetic relationships can be figured out are limited. No wonder that all the phylogenetic diagrams are liable to have many resemblances.

Perhaps the most interesting families of snakes, phylogenetically, are the so-called blind snakes — Anomalepididae, Typhlopidae, and

Leptotyphlopidae. They are small, highly adapted to a burrowing existence, and superficially resemble each other as well as many limbless lizards. Up to 1939 the anomalepidids had been included with the typhlopids, but Taylor in that year proposed the new family Anomalepididae by reasons of the cephalic squamation and the presence of teeth on both jaws. In comparison, *Typhlops* has an edentate lower jaw and *Leptotyphlops* has an edentate upper jaw.

McDowell and Bogert (1954) included the anomalepidids under the Typhlopidae (as Dowling also did later). Partly because of this surely erroneous inclusion certain of their conclusions are without good foundation. Their inadequate handling of the hyoid apparatus, treated in the first part of this paper, is a case in point. Underwood (1957) in his critique of the former's paper added a number of personal, and new, observations on the anatomy of blind snakes which serve to point up the need for a more thorough anatomical study of these animals.

McDowell and Bogert (1954) concluded that "typhlopids" are really not snakes; leptotyphlopids were included in the snakes, however. Moreover they believed that the typhlopids "are even more distinct from leptotyphlopids than from the typical snakes." However, at least four (Nos. 5, 6, 7, 10) of the ten features that they listed on p. 86 as being unique to "typhlopids" are actually based on anomalepidids. List (1966), after a thorough, comprehensive study of the skeleton of the blind snakes, was convinced that the anomalepidids deserve family rank. The work presented herein supports that view and furthermore tends to show that the anomalepidids are snakes, but have evolved along an entirely different line than the rest of the snakes.

The similarity in hyoids and associated muscles of *Leptotyphlops* and *Typhlops* has been shown; a common derivation is indicated. Underwood (1957) discussed similarities of the two families and decided that the two might well have diverged from a common ancestor.

List and Underwood, in their respective papers, both discounted most of McDowell and Bogert's differences of Typhlopidae from snakes in a broad sense. Again, the confusion caused by inclusion of the anomalepidids discounts some of McDowell and Bogert's points. Underwood presented a list of features in which *Typhlops* is definitely snakelike; e.g., the eye structure, thymus bodies, anal glands, platytrochial skull, and the facial artery's course. With such characters as these, plus presence of several snakelike characteristics of the ventral head musculature, viz. *hyotrachealis*, strong development of the *costocutaneous superior* fibers, and reduced *constrictor colli*, a case for including *Typhlops* with the snakes is definitely strong. This also holds for *Leptotyphlops*.

In looking among the lizards for some clues as to the ancestry of snakes, several problems are immediately evident. One is that since modern snakes have evolved, or changed, from their ancestors, then it is only fair to suggest that the lizards which gave rise to these ancestors also have changed to some degree. Therefore, it is hard to believe that we can discover the ancestors to the serpents among the modern species of lizards. But, of course, we may find evidence that certain living species of lizards are the probable descendants of the ancestors of snakes. In effect, by studying the modern species one is only observing the current end points of evolution in snakes and lizards.

Another problem which obscures the attempt to unravel the origin of snakes is that of convergence. There are many examples of this between lizards and snakes: loss of limbs and girdles, skull modifications of various sorts, etc.

No lizard is particularly like snakes in both the hyoid and the ventral head muscles. However, *Anniella*, of the anguinomorph family Anniellidae, has a simple, inverted Y-shaped hyoid, obviously composed of a basihyal with lingual process, and two attached 1st ceratobranchials, which is very similar to that of *Leptotyphlops* and *Typhlops*. The musculature includes the *genioglossus*, divergent *hyoglossi*, a well-developed *sternohyoideus* (which possibly might be an *omohyoideus*), a broad *ceratomandibularis* with a *neuromandibularis* partially attached, *constrictor colli* not attached to hyoid, and broad transverse intermandibulars; there is no laryngeal protractor or retractor.

The musculature does not precisely recall the condition in any snake, including *Typhlops* and *Leptotyphlops*. Naturally the main difference is that *Anniella* lacks the *hyotrachealis*, as well as the *geniotrachealis*—both present in the snakes. Excluding these important differences, there is at least some resemblance to the typhlopids in muscles present. There is also a certain similarity to *Cylindrophis*, which lacks, though, the *sternohyoideus* (*omohyoideus*?) found in *Anniella*. Loss of the basihyal of the anniellid hyoid would certainly leave a hyoid structure very much like that in *Cylindrophis* (and others), of course.

But although *Anniella* shows other snakelike tendencies, such as the eye covered by a scale, loss of temporal arches, and near limblessness, it still retains enough lizard ones to suggest only convergence with snakes rather than close relationship.

McDowell and Bogert (1954) suggested that "snakes are derived from platynotan (*Varanus*-like) lizards." In particular they found that *Lanthanotus* is very similar to *Leptotyphlops* in many ways. With respect to varanid-like lizards as snake ancestors, Underwood (1957)

found fault in many points, and finally decided that it was, in 1957, too early in the course of phylogenetic studies to decide upon the ancestry of snakes. It is probably still too early.

The hyoid and associated muscles in *Varanus*, as well as in most lizards, are much more elaborated than in snakes. Comparison of *Varanus* with snakes reveals that if a series of losses and reductions in the hyoid anatomy of *Varanus* were made, a possible snakelike type could be produced. The trouble with this view is that the same could be said about a great many lizards! A point, though, that may indicate modern varanids have evolved from types close to the ancestry of snakes is the presence of a laryngeal protractor, which has not yet been found in other lizards.

There is a considerable amount of literature concerning the ancestry of snakes. Much of this literature has centered on trying to derive the snakes from platynotan lizards. The subject of the origin of snakes has only been touched upon in this paper. The most comprehensive review of the literature on the subject is by Bellairs and Underwood (1951), who, themselves, were not at all convinced that snakes were derived from platynotan lizards; Underwood (1957) later re-emphasized that stand.

B. Summary

1. Characteristics of the hyoid and its associated musculature are listed for the recognized families of snakes, and for the lizard *Varanus*.
2. Primitive snake stock might have had this anatomy: hyoid of basihyal, hypohyals and ceratohyals, 1st and 2nd ceratobranchials; two ramus-hyoid muscles, at least two girdle-hyoid muscles, *hyotrachealis*, *geniotrachealis*, *costocutaneus superior* attaching to mandibles, *constrictor colli*, transverse intermandibulars.
3. A phylogenetic tree for snakes has been worked out on the basis of their hyoid anatomy. This tree consists of a more or less main stem or stock from which six lines of snakes have evolved.
4. The first line gave rise to the anomalepidids with their distinctive "M" type hyoid and *geniohyoideus*, etc.
5. The stock lost the 2nd arch cornua. From this new stock evolved the line which gave rise to the typhlopids and leptotyphlopids, with their distinctive "Y" type hyoid and *sternohyoideus*, etc.
6. The stock lost the *sternohyoideus* and gained the *costomandibularis*. A third, small line gave rise to the uropeltids, with their reduced "V" type hyoid and *intermandibularis anterior*.

7. A fourth line emerged from the stock to give rise to the aniliids, also with a reduced "V" hyoid, and with a broad *ceratomandibularis*.

8. A major event in the phylogeny was the formation of the *neurocostomandibularis*. The stock itself had a reduction in the *intermandibularis anterior* and formed the fifth line, which gave rise in one direction to the true boids and xenopeltids, with a "V" hyoid type, and in another direction to the genera *Bolyeria*, *Casarea*, *Trachyboa*, and *Tropidophis*, with their parallel hyoid.

9. The sixth line, given off from the stock with the *neurocostomandibularis*, lost the 1st ceratobranchials; this line gave rise to the colubrids, elapids, hydrophids, viperids, and crotalids, with their parallel hyoid and large, angular intermandibulars.

10. Reductions and losses have largely characterized the above phylogenetic tree. Only the *costomandibularis* is a "new" muscle and it is only a modification of one already present.

11. A brief discussion is given of other recent efforts in phylogenetic studies of snakes.

12. The thesis that anomalepidids are distinct from typhlopids, and the thesis that these two families are snakes, are substantiated.

13. The past, generally unsatisfactory search among modern lizards for the ancestors of snakes is not helped much by the study of the hyoid anatomy. It seems obvious that both modern snakes and lizards have changed to some degree from their antecedents, making the search very difficult.

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Explanation for Figures

The head muscle figures are of the ventral view unless otherwise stated. Abbreviations used in the figures are:

bhy	basihyal	hgl	<i>hyoglossus</i>
Icb	1st ceratobranchial	hhy	hypohyal
IIcb	2nd ceratobranchial	htr	<i>hyotrachealis</i>
cei	<i>costocutaneus inferior</i>	ima	<i>intermandibularis anterior</i>
ces	<i>costocutaneus superior</i>	imp	<i>intermandibularis posterior profundus</i>
cer	<i>ceratomandibularis</i>	ims	<i>intermandibularis posterior superficialis</i>
cer'	<i>ceratomandibularis, medial slip</i>	int	<i>obliquus abdominis internus</i>
chy	ceratohyal	neu	<i>neuromandibularis</i>
cmn	<i>cervicomandibularis</i>	omo	<i>omohyoideus</i>
col	<i>constrictor colli</i>	pro	<i>processus lingualis (lingual process)</i>
con	<i>constrictor of submandibular gland</i>	rq	<i>retractor quadratus</i>
cos	<i>costomandibularis</i>	sh	sheath of tongue
dil	<i>dilator of submandibular gland</i>	ste	<i>sternohyoideus</i>
ex	unnamed muscle	step	<i>sternohyoideus profundus</i>
geh	<i>geniohyoideus</i>	stes	<i>sternohyoideus superficialis</i>
geh'	<i>geniohyoideus, medial slip</i>	sub	<i>submandibular gland</i>
ggl	<i>genioglossus</i>	tbr	<i>transversus branchialis</i>
ggl'	<i>genioglossus, medial slip</i>		
gtr	<i>geniotrachealis</i>		

FIGURE 1. Various hyoids (some with only one side shown). Figures A-G are lizards; H, J-M are snakes.

A — Varanidae: *Varanus* (from Gnanamuthu).

B — Iguanidae: *Anolis chrysolepis* (from Beebe) $\times 6$. A complete lizard hyoid.

C — Amphisbaenidae: *Amphisbaena darwini* (from Richter) $\times 10$.

D — Anguidae: *Gerrhonotus multicarinatus* (from Cope).

E — Geckonidae: *Gehyra oceanica* (from Richter) $\times 2$.

F — Scincidae: *Mabouia carinata* (from Richter) $\times 2$.

G — Xenosauridae: *Xenosaurus grandis* (from Camp) $\times 2$.

H — Anomalepididae: *Liotyphlops albirostris* $\times 15$. "M" type.

J — Typhlopidae: *Typhlops schlegeli mucruso* $\times 11$. "Y" type.

K — Leptotyphlopidae: *Leptotyphlops maximus* $\times 7$. "Y" type.

L — Boidae: *Sanzinia madagascariensis* $\times 2\frac{1}{2}$. "V" type.

M — Crotalidae: *Bothrops mexicanus* $\times 1\frac{1}{2}$. Parallel type.

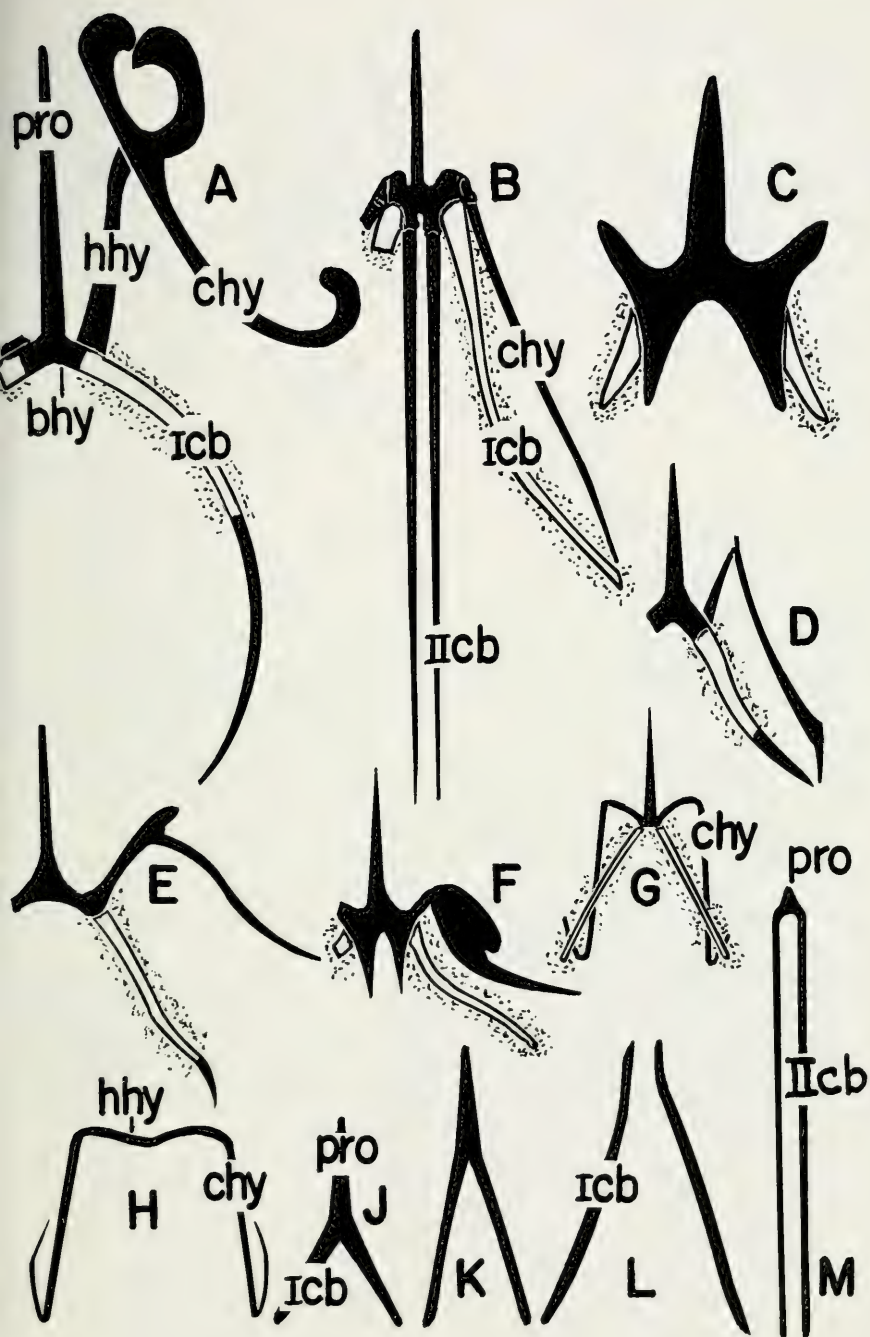


FIGURE 2. Various hyoids. A-E are lizards; F-H, J, K are snakes. Rib ends are shown in the figures of snake hyoids. The bar represents 1 mm.

A — Anniellidae: *Anniella pulchra* (from Cope). Hypohyals and ceratohyals not present.

B — Lanthanotidae: *Lanthanotus borneensis* (after McDowell and Bogert).

C — Anguidae: *Anguis fragilis* (from Cope).

D — Helodermatidae: *Heloderma suspectum* (from Cope).

E — Amphisbaenidae: *Rhineura floridana* (from Cope). Ceratohyals probably not present.

F — Typhlopidae: *Typhlops reticulatus* (from List) $\times 18$. Note separation of 1st ceratobranchials from basihyal.

G — Typhlopidae: *Typhlops pusillus* (from List) $\times 18$. 1st ceratobranchials only.

H — Typhlopidae: *Typhlops polygrammicus* (from List) $\times 8$. Basihyal alone?

J — Leptotyphlopidae: *Leptotyphlops dulcis dissectus* (from List) $\times 20$.

K — Leptotyphlopidae: *Leptotyphlops phenops* (from List) $\times 8$.

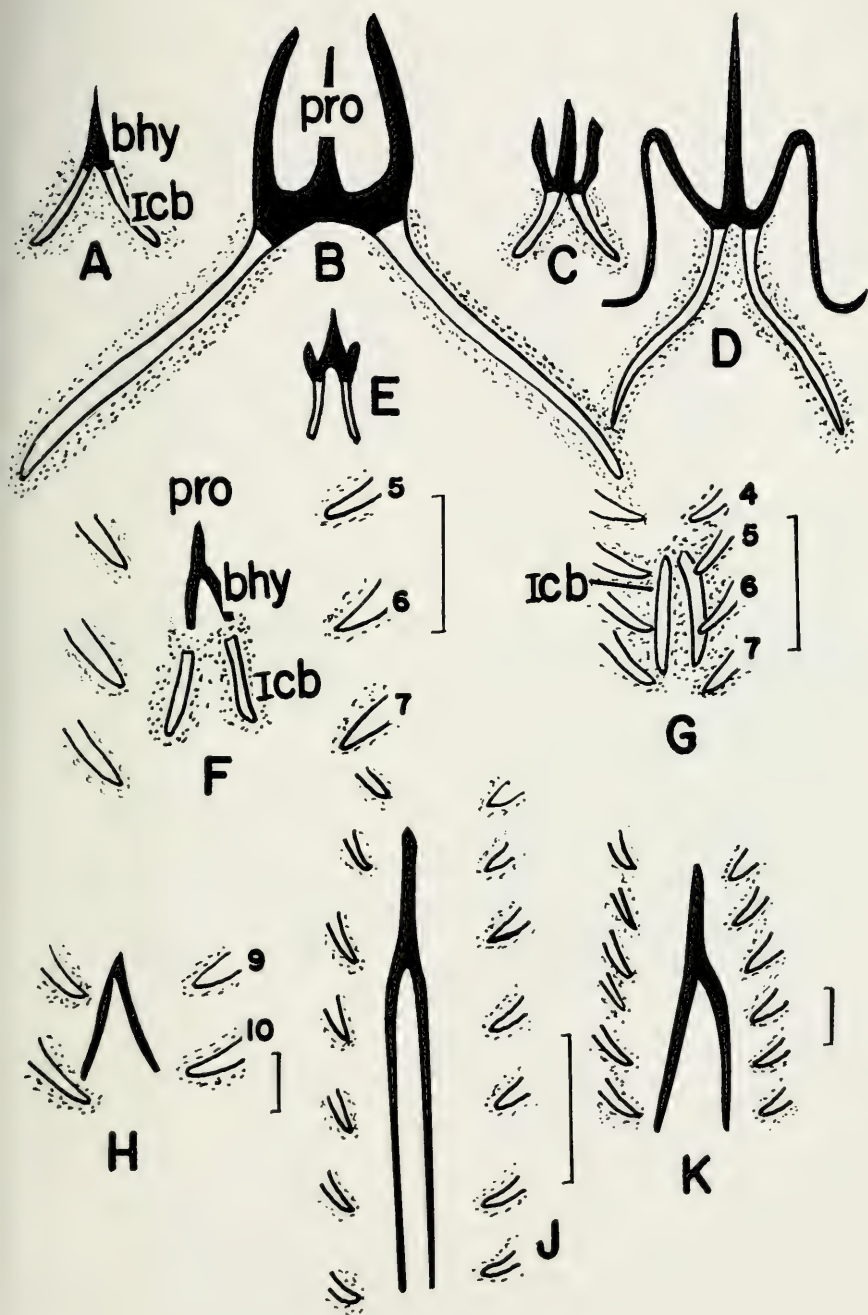


FIGURE 3. Various snake hyoids (from Smith and Warner). Sequential dashes at left of drawing are corresponding ventral margins. The bar in drawing H represents 10 mm. All drawings are approximately natural size.

A — Colubridae: *Salvadora grahamiae hexalepis*.

B — Colubridae: *Opheodrys vernalis*.

C — Colubridae: *Storeria dekayi*.

D — Colubridae: *Sibynomorphus catesbyi*.

E — Colubridae: *Tropidonotus natrix*.

F — Colubridae: *Tantilla gracilis*.

G — Colubridae: *Sonora s. semiannulata*.

H — Elapidae: *Micrurus fulvius*.

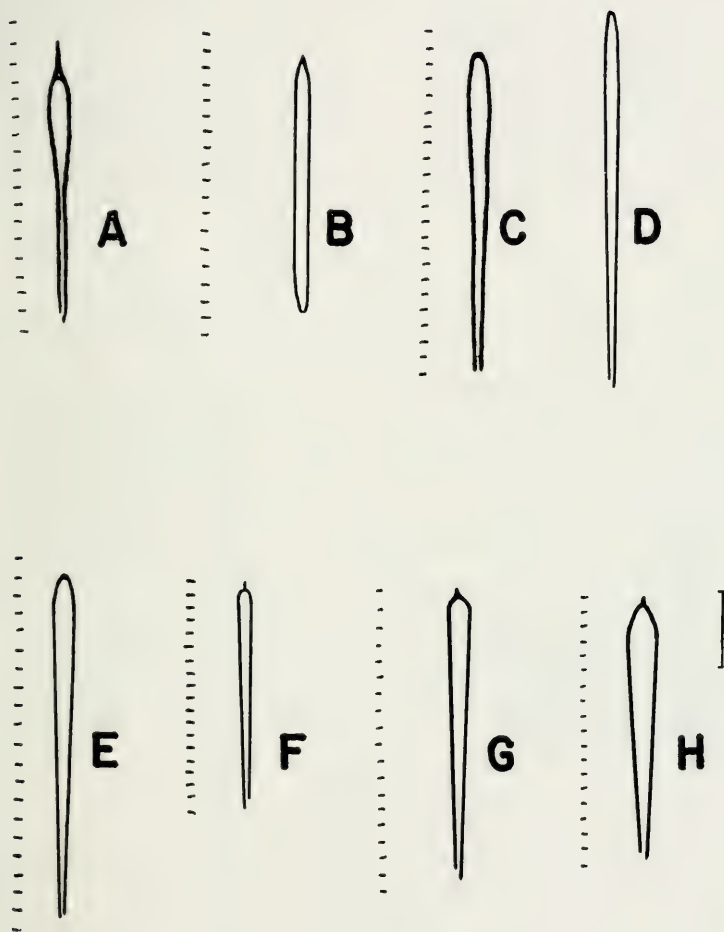


FIGURE 4. More hyoids of various snakes (also from Smith and Warner). All drawings are approximately natural size. These genera are all colubrids.

- A — *Elaphe guttata*.
- B — *Lampropeltis d. doliata*.
- C — *Diadophis punctatus edwardsii*.
- D — *Cerberus rhynchops*.
- E — *Farancia abacura reinwardtii*.
- F — *Coluber constrictor priapus*.
- G — *Natrix s. sipedon*.
- H — *Chersydrus granulatus*.
- J — *Rhadinaea flavilata*.

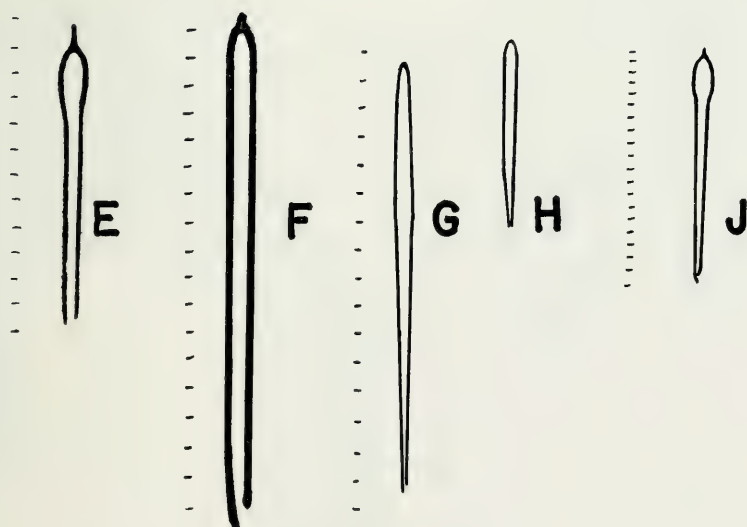
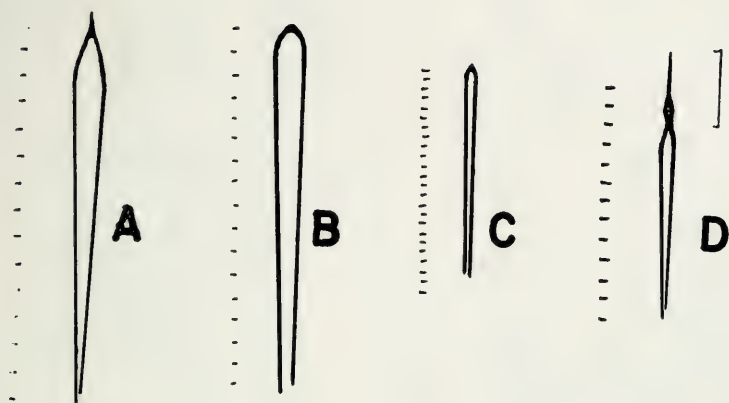


FIGURE 5. Anniellidae: *Anniella pulchra nigra* (UI 4460); an anguinomorph lizard.

A — Ventral view. The *constrictor colli* is removed on both sides. The right side shows the deep layer. The posthyoid muscle named the *sternohyoideus* (ste) may be the *omohyoideus*. Note the simplified hyoid with only the 1st ceratobranchials present as cornua. $\times 13$

B — Right lateral view. There is a snakelike arrangement of the *cervico-mandibularis* (cmn), and of what seems to be the *neuromandibularis* (neu). Note the slender cartilage, which apparently represents the scapula-procoracoid, to which attaches the muscle designated as the *sternohyoideus*. $\times 7$

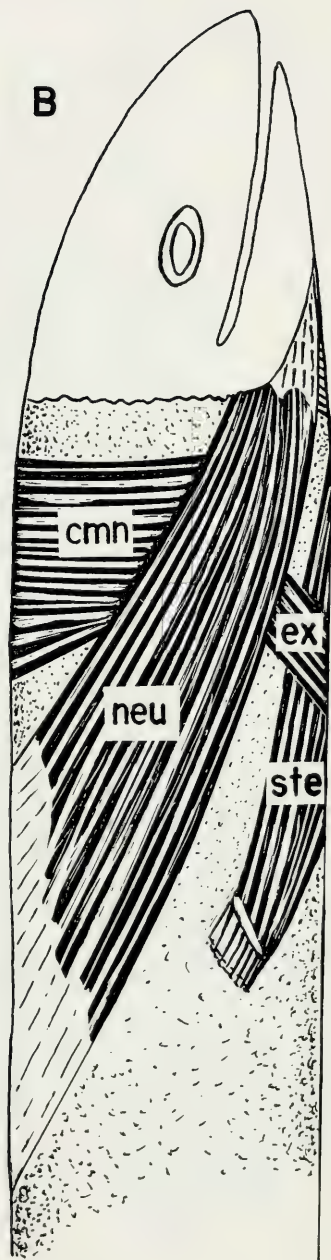
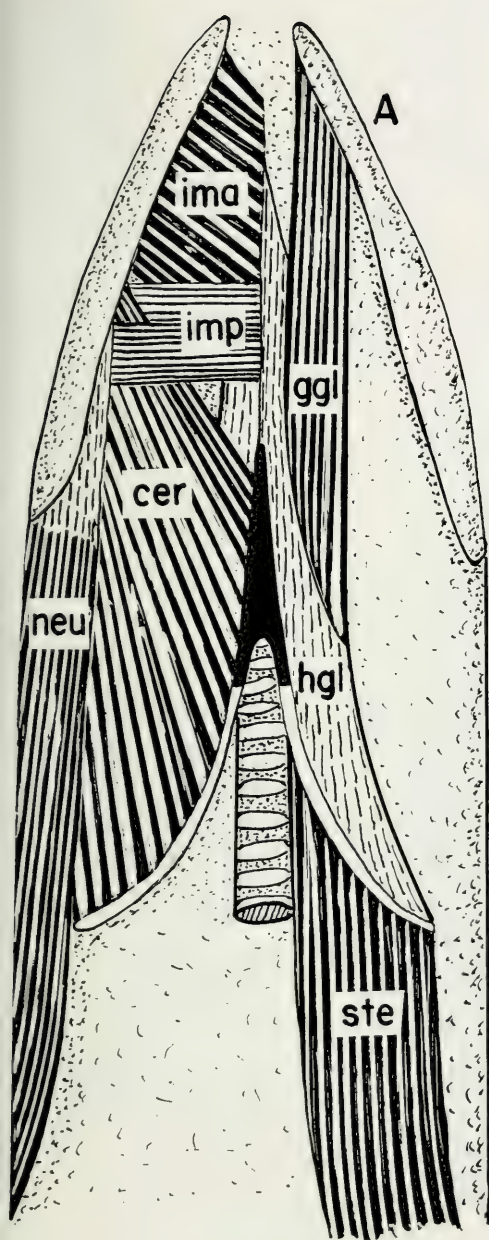


FIGURE 6. Varanidae: *Varanus monitor* (UI 37536); a platynotan anguimorph.

A — Right lateral view. Note the distinct cervicomandibular and neuromandibular muscles, and the hyoid with two pairs of cornua. $\times 2.5$

B — Ventral view. The *constrictor colli* and intermandibulars are removed. Middle layer at left, deep at right. Note the two pairs of the *geniohyoideus* (geh and geh') inserting on the ceratohyal, and the *neuromandibularis* partially inserting into the *ceratomandibularis* (cer). The presence of a *geniotrachealis* (gtr) without a *hyotrachealis* is interesting and unique. $\times 3.2$

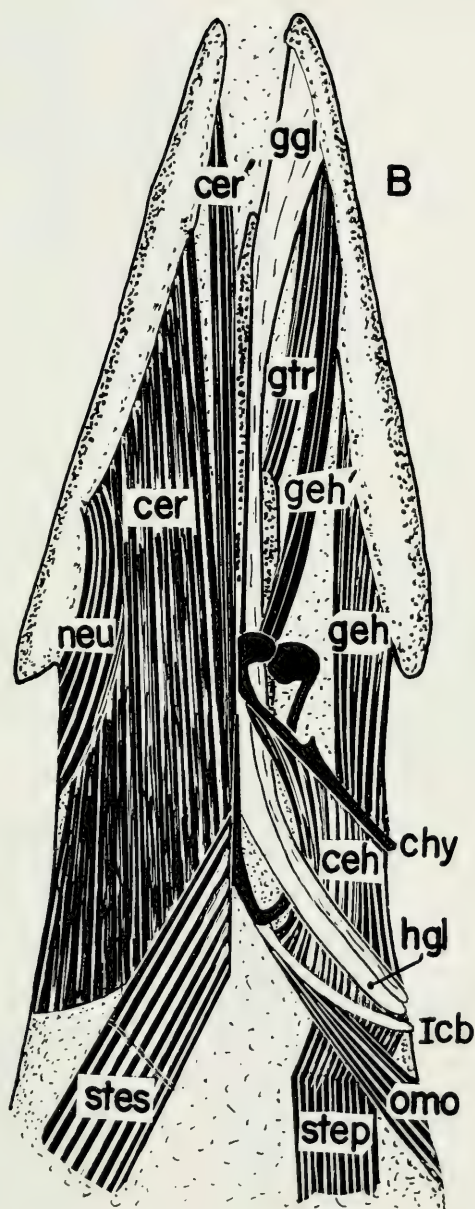
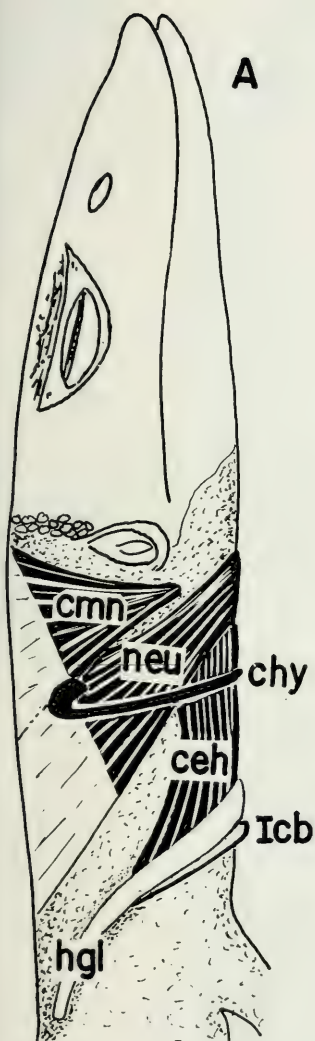


FIGURE 7. Anomalepididae: *Liotyphlops albirostris* (MCZ 25232) $\times 27$. Note the heavy *geniotrachealis* (gtr). The *hyotrachealis* (htr) attaches posteriorly to the buccal floor. The intermandibulars are broad and generally transverse. The *geniohyoideus* is prominent and runs between the lower jaw and the hypohyal and ceratohyal. A slender muscle which is marked "cer" may well represent a greatly reduced *ceratomandibularis*; it attaches posteriorly to the recurrent cornu; the 1st ceratobranchial is of course missing in this family. The *hyoglossus* (hgl) attaches posteriorly to the ceratohyal.

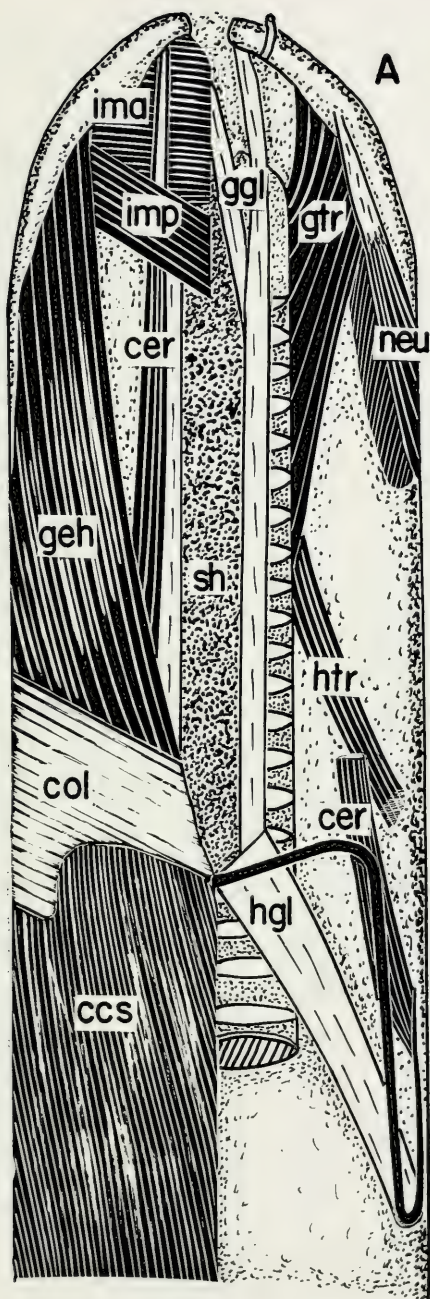


FIGURE 8. Typhlopidae: *Typhlops bibroni* (CNHM 17718) $\times 7$.

A — The *costocutaneus superior* muscles (ccs) are entirely removed in the main figure, but are shown intact in the lower left inset. The intermandibulars (ima and imp), *constrictor colli*, and *neuromandibularis*, are removed at the right. The *sternohyoideus* is completed in (B). The slender tendon of the *ceratomandibularis* is shown at the left; it is sectioned at the right.

B — Detail of the hyoid and the attached muscles. The fibers of the *sternohyoideus* attach posteriorly to the midventral raphe. Note that the fibers of the *hyoglossi* are always parallel and attach directly to the cornua.

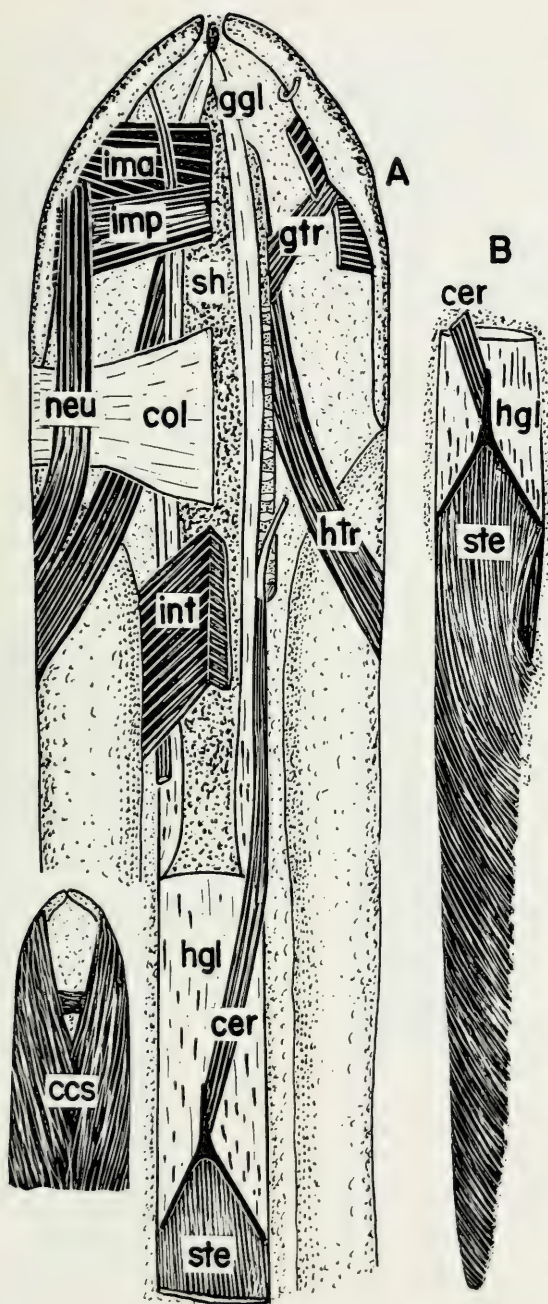


FIGURE 9. Typhlopidae: *Typhlops schlegeli mucruso* (CNHM 81018).

A — *Costocutaneus superior* is removed. Deep layer is at the right. Note that the *hyotrachealis* (htr) has a posterior attachment over the rib cage. $\times 7$

B — Completion of the tongue and *hyoglossi*, and showing the hyoid with attached muscles. The sternohyoid fibers affix posteriorly to the midventral raphe, but some of the fibers end blindly. Details of the sternohyoid attachments to the hyoid are shown in the two small figures at the right. $\times 7$

C — The *costocutaneus superior* is shown intact. $\times 3.5$

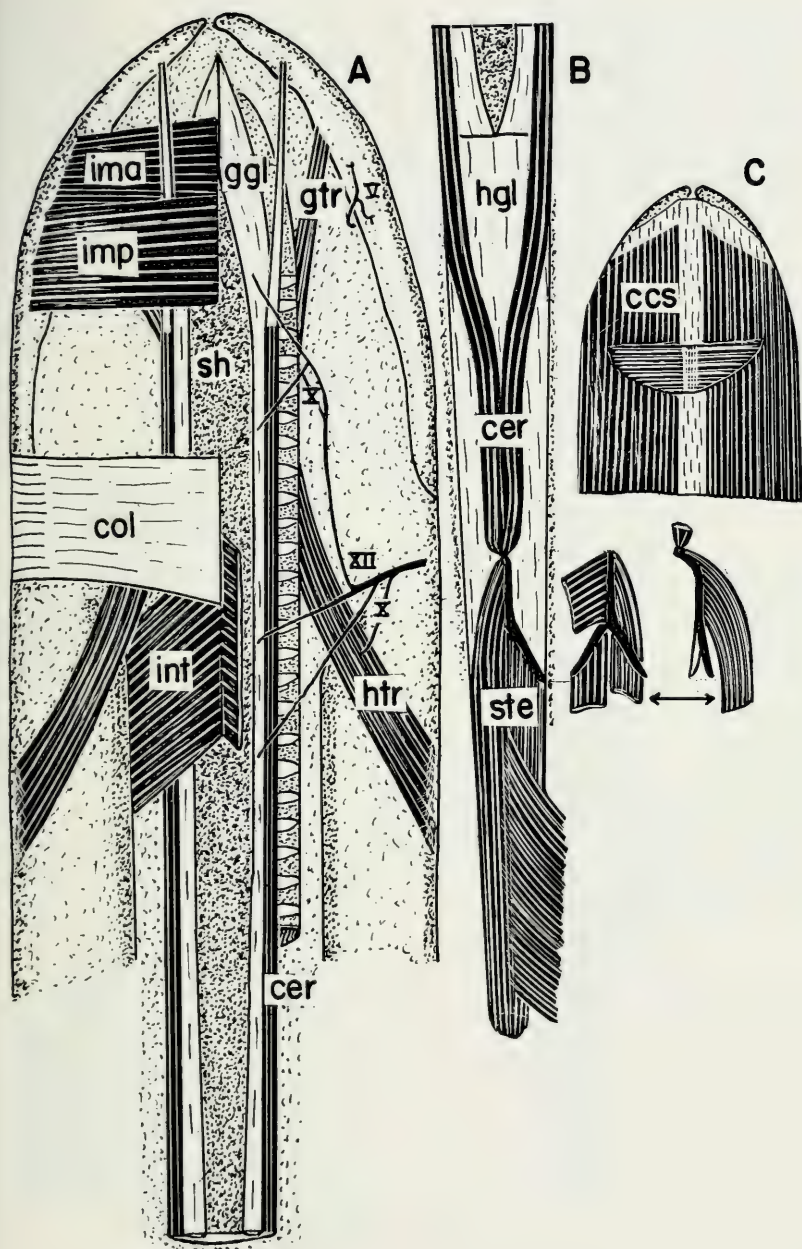


FIGURE 10. Leptotyphlopidae: *Leptotyphlops maximus* (CNHM 38282) $\times 11$.

A — *Costocutaneus superior* is removed. Deep layer is at the right. *Obliquus internus* (int) is removed at the right. The small inset at lower left shows the *costocutaneus superior* intact; note the sample of ventral scale impressions on the muscle.

B — Completion of the tongue and *hyoglossi*, and the *sternohyoideus*, which has been shortened for the figure. Part of the sternohyoid fibers attach to the midventral raphe, but the rest end blindly.

C — *Genioglossus* and *sternohyoideus* removed to show the bifurcate *hyoglossi* and their relation to the hyoid. The hyoglossal fibers are parallel to the cornua and are also encapsulated.

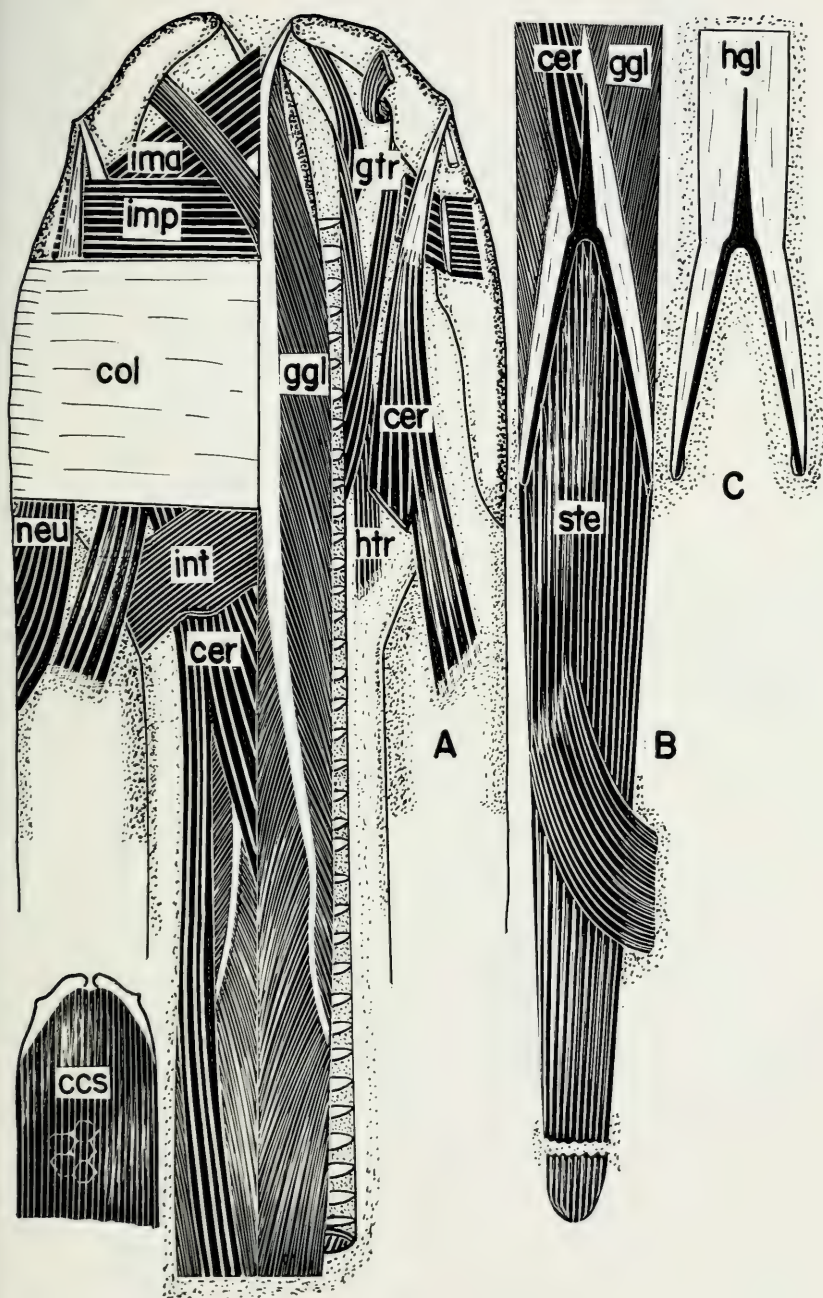


FIGURE 11. Uropeltidae: *Rhinophis blythi* (CNHM 25930) $\times 12$. The origin of the *costocutaneus superior* on the jaw remains at the right. Note the large *omohyoideus*-like muscle (omo). The *intermandibularis anterior* (ima) is represented by a thin tendon. The *neuromandibularis* is separate, and the *cera-tomandibularis* is reduced. The inset shows the *costocutaneus superior* intact.

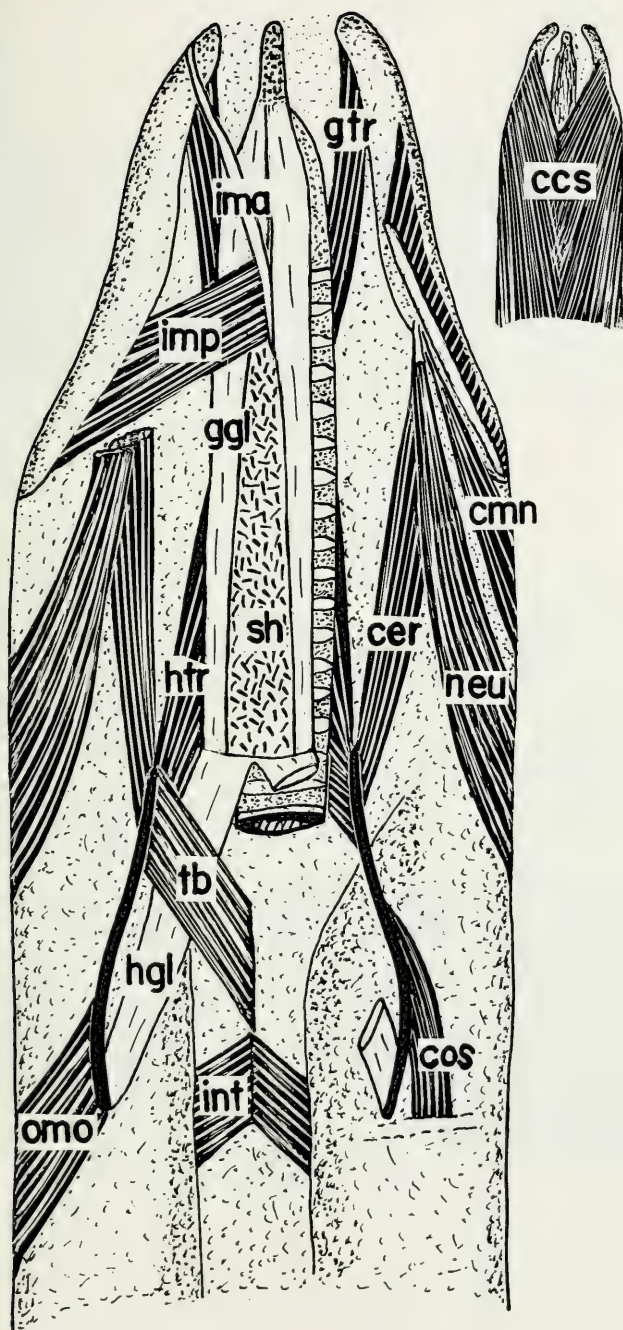


FIGURE 12. The following all belong to the Aniliidae.

A — *Anilius scytale* (CNHM 35683) $\times 2.5$. The *hyotrachealis* and the *transversus branchialis* (tb) are sectioned at the right. The *costomandibularis* (cos) is present. The *neuromandibularis* is separate. Note that there is no *intermandibularis anterior*.

B — *Cylindrophis rufus* (CNHM 67269) $\times 3$. The *costocutaneus superior* is cut at the left. Note that some fibers of the *ceratomandibularis* run between the cornua to end at the midventral raphe. The transition from *costocutaneus inferior* (cci) to *costomandibularis* is shown. The *intermandibularis anterior* is a very slender muscle. The inset shows the hyoid and its attached muscles in detail.

C — *Cylindrophis maculatus* (MCZ 15795) $\times 5$. The *costocutaneus superior* is cut at the left. The hyoid cornua are much reduced and so are the *ceratomandibular* slips attaching to each cornu. The *costomandibularis* joins the *ceratomandibularis*, but the *neuromandibularis* is still separate. The *intermandibularis anterior* is small.

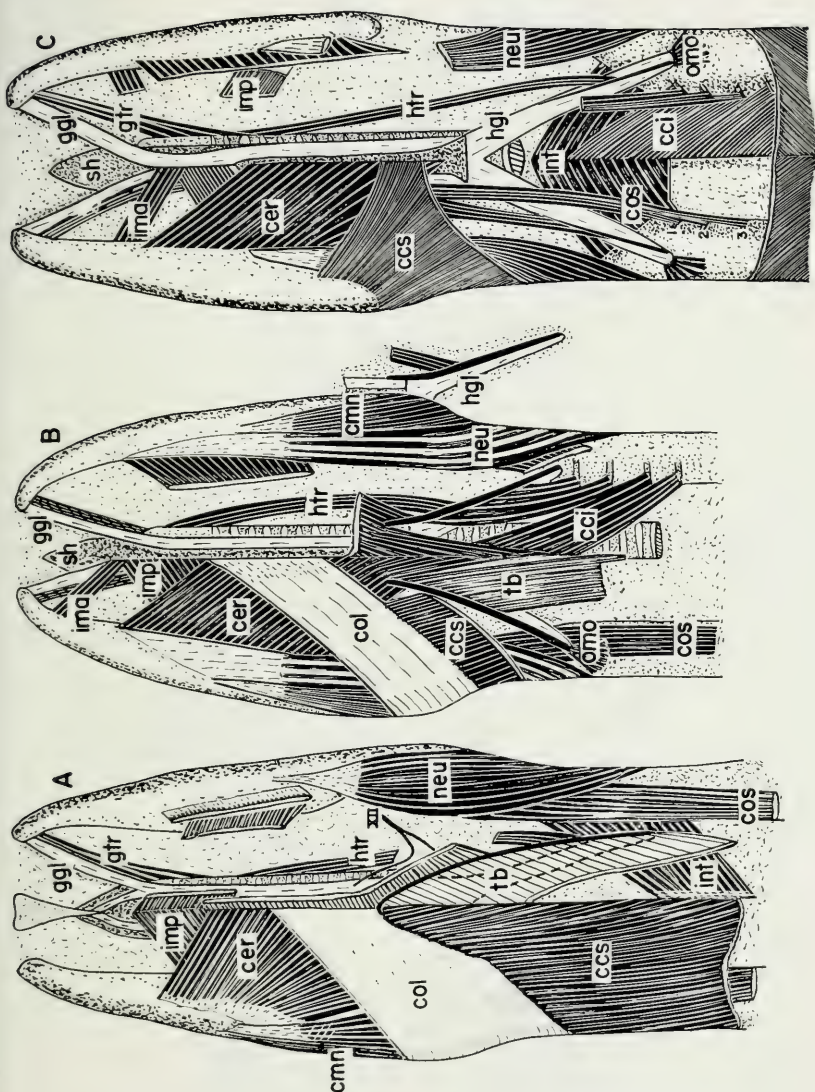


FIGURE 13. Xenopeltidae: *Xenopeltis unicolor* (CNHM 15273) $\times 3.5$. Note the lack of an *intermandibularis anterior*. The most important thing to observe is the presence of a *neurocostomandibularis* muscle, a complex which is contributed to by the *ceratomandibularis*, *neuromandibularis*, and *costomandibularis*. Note, however, that the costomandibular slip lies deep to the other two contributing muscles.

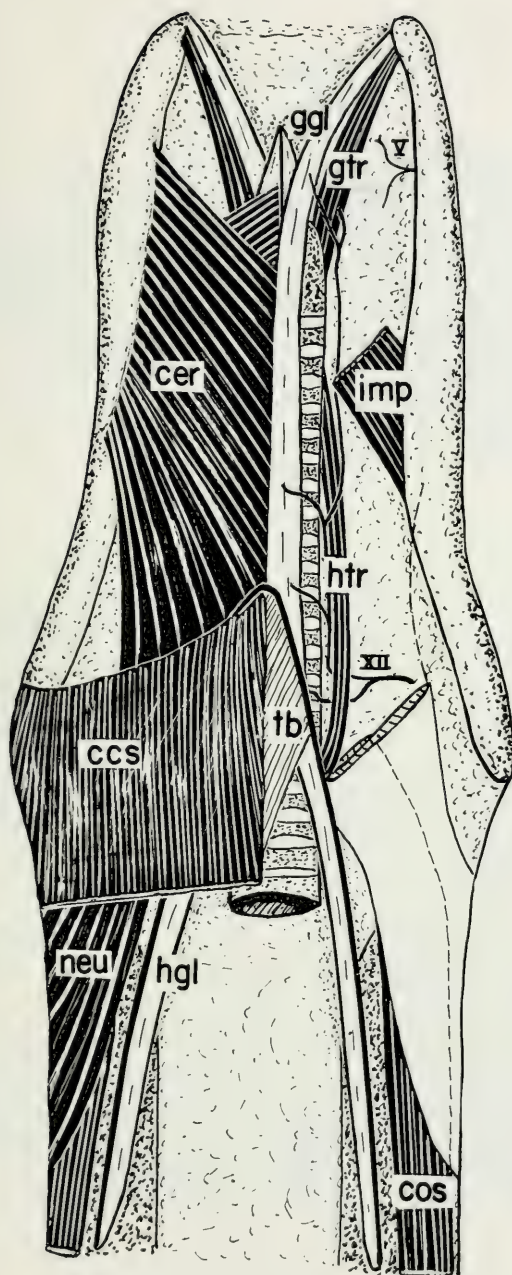


FIGURE 14. The following all belong to the Boidae (*sensu stricto*).

A — *Python sebae* $\times 2.4$. Most *costocutaneus superior* fibers are removed. The basihyal is definitely lacking. The *intermandibularis anterior* is weak. There is still some overlap in the neurocostomandibular complex.

B — *Eryx c. colubrinus* (CNHM 81224) $\times 2.4$. All *costocutaneus superior* fibers are removed; they attach to the hyoid. There is a small muscle present which is conveniently called the *omohyoideus*. Note the spinal nerves lying upon the *internal oblique*. The inset at the right shows the *hyoglossus* and hyoid relationship plus the attachment of the *hyotrachealis*.

C — *Epicrates cenchris* (CNHM 31143) $\times 1.9$. The *costocutaneus superior* fibers are particularly well shown here at left; ventral scale impressions upon the fibers are illustrated. Note the well-developed *neurocostomandibularis*. The *costomandibularis* has two slips. The inset at the right shows the attachments of the *hyotrachealis* and the *hyoglossus* to the hyoid cornu.

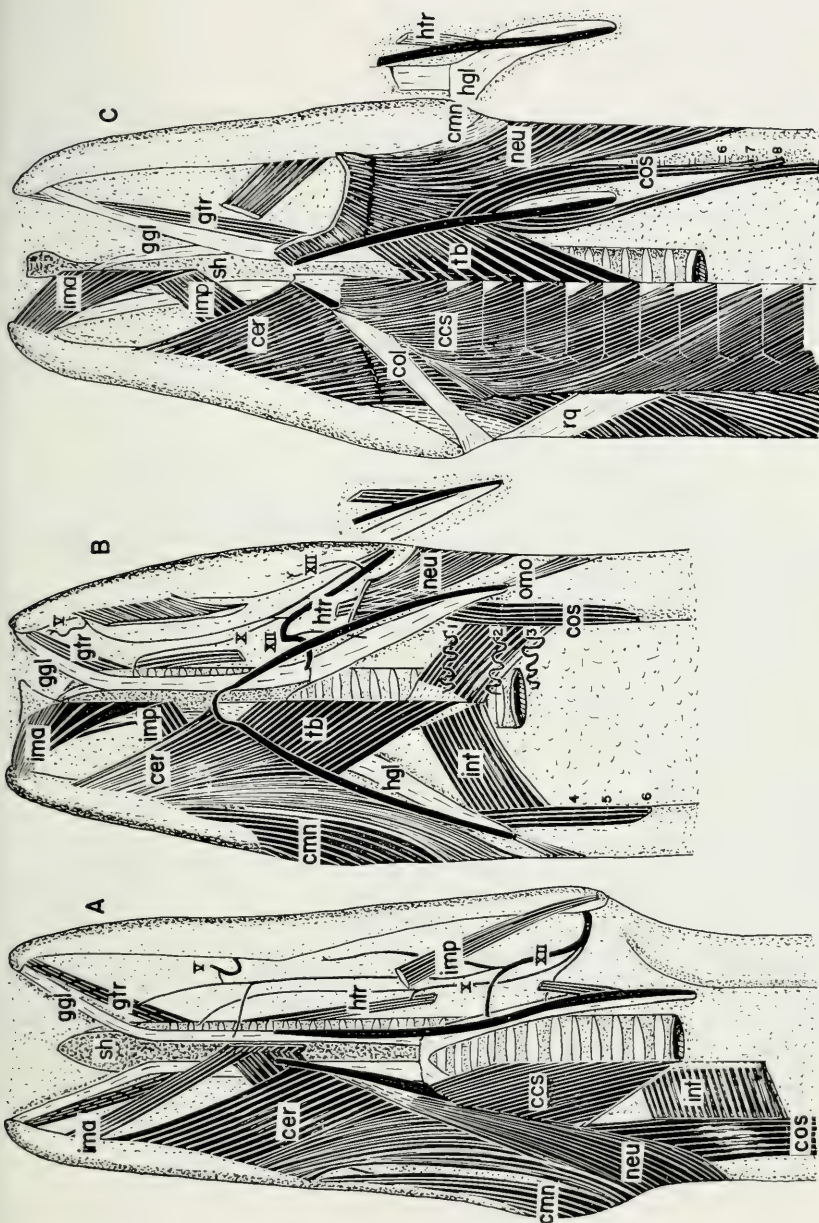


FIGURE 15.

A — Boidae (*sensu lato*): *Tropidophis maculatus* (USNM 56328) $\times 4.6$. Note the weak *intermandibularis anterior*. The parallel type of hyoid and the juxtaposed *hyoglossi* are of course important to notice. The *neurocostomandibularis* is well developed and essentially presents a single layer. The *hyotrachealis* is omitted from the figure.

B — Colubridae: *Achrochordus javanicus* (CNHM 67268) $\times 3.2$. This colubrid has a remarkable set of independent variations: the very expansive *costocutaneus superior*, with which the *cervicomandibularis* (not shown) partially intertwines laterally; the independent *ceratomandibularis*; there seems to be no *neuromandibularis* or *costomandibularis*. The hyoid and *hyoglossi* are not shown completely, and the *hyotrachealis* is omitted. The intermandibulars are relatively very large in this species.

C — Colubridae: *Atretium schistosum* (MCZ 1330) $\times 3.7$. Note the *intermandibularis posterior superficialis* (ims) and the strong *intermandibularis anterior*. There is a well-formed *neurocostomandibularis* with a distinct inscription. The hyoid cornua and *hyoglossi* are incomplete in the figure.

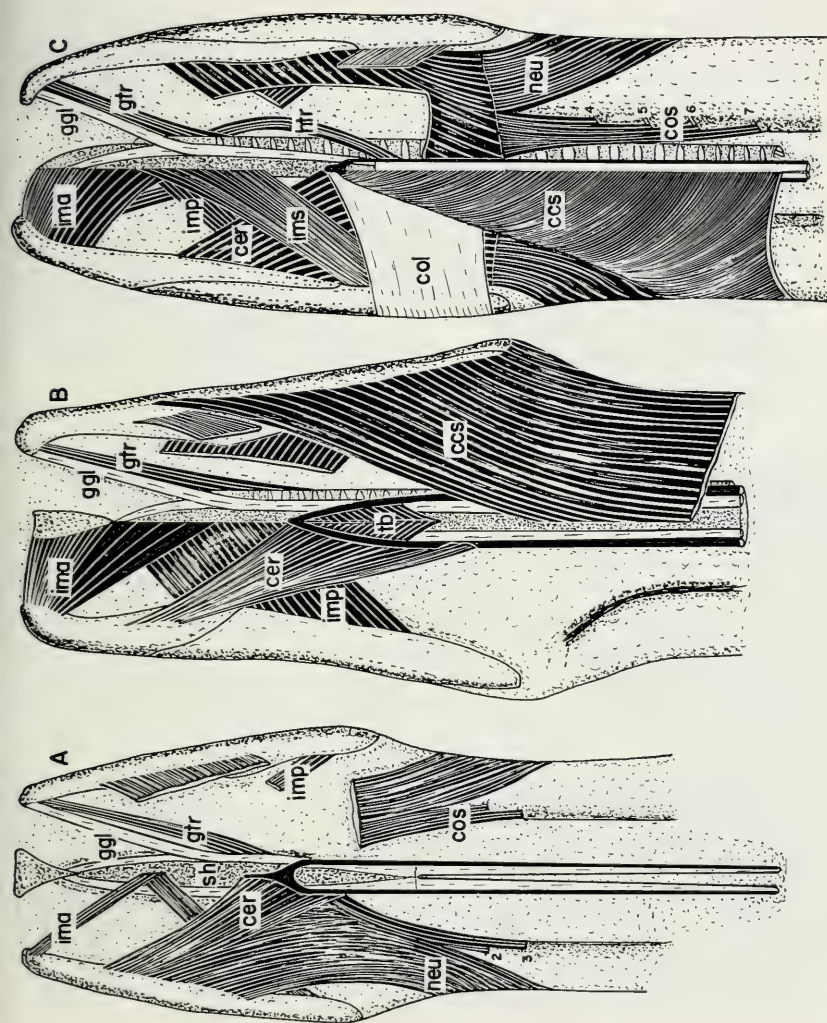


FIGURE 16. The following all belong to the Colubridae.

A — *Heterodon p. platyrhinos* $\times 2$. Note the origin of the *costomandibularis* from ribs 1-8, which are shown free from parietal muscles. The first slip of the *costocutaneus inferior* is from rib 9. A small slip of the *ceratomandibularis* passes external to the cornu to insert on the midventral raphe. The *hyotrachealis* is not shown. The hyoid and the *hyoglossi* are incomplete posteriorly.

B — *Thamnophis s. sirtalis* $\times 3.4$. A right lateral view. Note the distinct tendinous inscription in the *neurocostomandibularis*. The *constrictor colli* is very thin.

C — *Thamnophis elegans vagrans* $\times 2.5$. The innervation pattern is rather completely shown; the common nerve trunk, composed of nerves X and XII (and IX), is illustrated. The upper right inset shows a submandibular gland with its *dilator* and *constrictor* muscles. The lower right inset shows the split origin of the *hyotrachealis*; the *ceratomandibularis* is shown transparent; one head of the *hyotrachealis* attaches to the tendinous inscription of the *neurocostomandibularis*. The hyoid and *hyoglossi* are incomplete posteriorly.

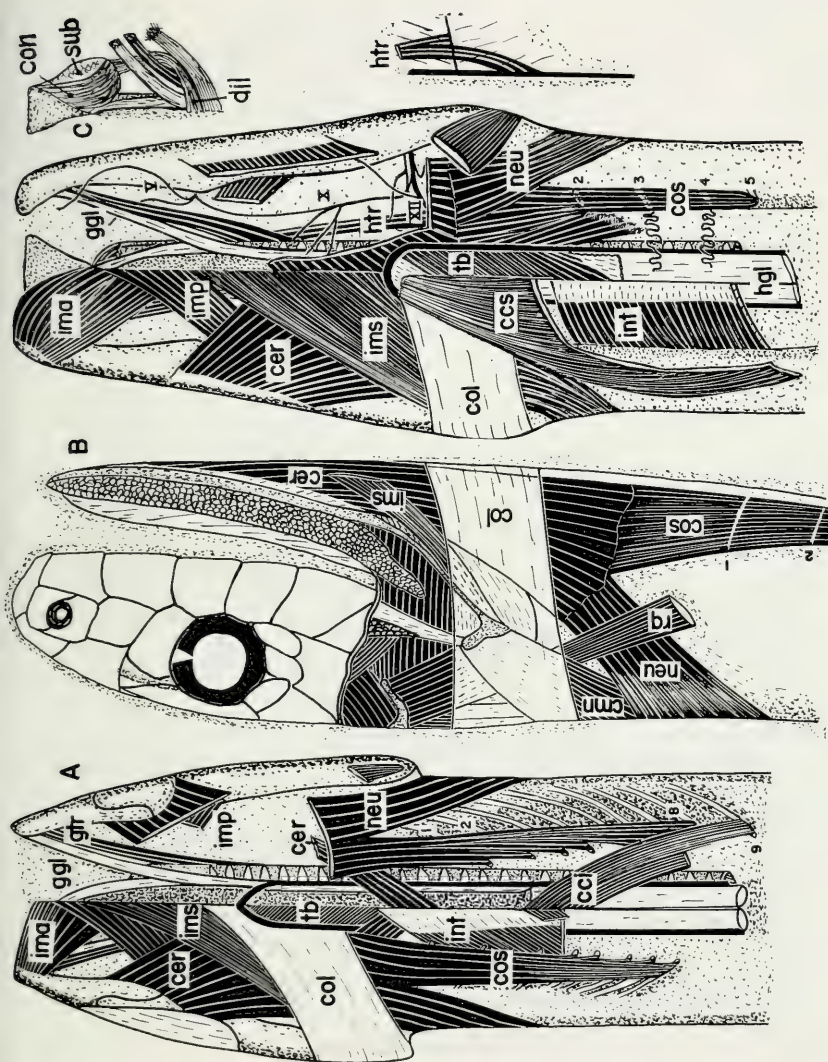


FIGURE 17.

A — Elapidae: *Denisonia par* (CNHM 41978) $\times 2.3$. The nerves are clearly shown, particularly the large branch to the tongue entering just anterior to the junction of the *hyoglossus* with the tongue sheath.

B — Hydrophidae: *Aipysurus eydouxi* (CNHM 11572) $\times 3.4$. There is no apparent *constrictor colli*. Note the *ceratomandibularis* at the left and the way part of it interleaves once with the *intermandibularis posterior profundus* (imp). The *cornua* and *hyoglossi* are incomplete in the figure.

C — Viperidae: *Cerastes vipera* (CNHM 63115) $\times 1.8$. There is no dissectable *constrictor colli*. Many of the nerves are shown. Note the *intermandibularis posterior superficialis*.

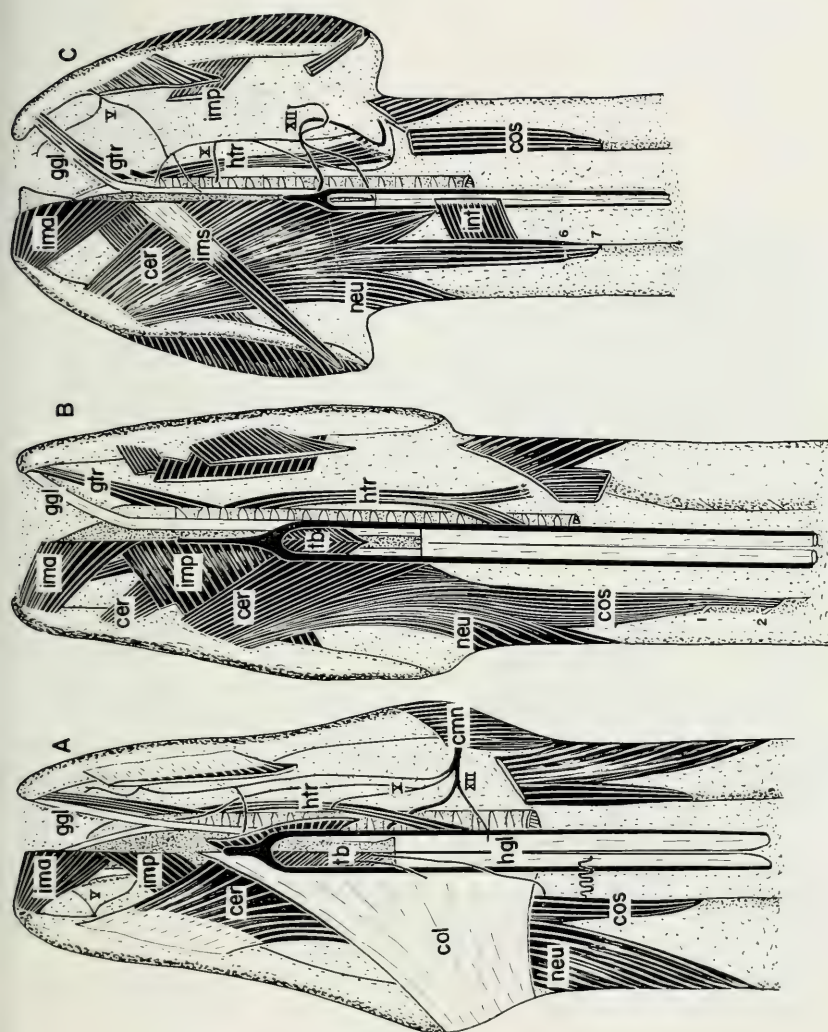


FIGURE 18.

A — Crotalidae: *Bothrops mexicanus* $\times 1.4$. The *intermandibularis posterior superficialis* is large.

B — A drawing of the ventral head region in a hypothetical primitive snake, whose anatomy of the region is suggested by structures found in living snakes and lizards. While this is only a presumed construction, it does satisfy conditions which have been indicated by a study of the hyoid and associated muscles in snakes. Note: the complete type of hyoid — basihyal, hypohyals, ceratohyals, 1st and 2nd ceratobranchials; the broad *constrictor colli* (inset); two ramus-hyoid muscles — *ceratomandibularis* and *geniohyoideus*; at least two posthyoid muscles — *sternohyoideus* (shown in two layers here, *superficialis* and *profundus*), and *omohyoideus*; a separate *neuromandibularis*; the *hyotrachealis*, which attaches to the buccal floor; the broad, largely transverse intermandibulars. The inset also shows a probably extensive *costocutaneus superior* which likely would lie superficial to the hyoid. The *sternohyoidei* and the *omohyoideus* are shown incomplete posteriorly.

The *hyoglossi* are divergent and attach to the 1st ceratobranchials, which are presumed to have been bony.

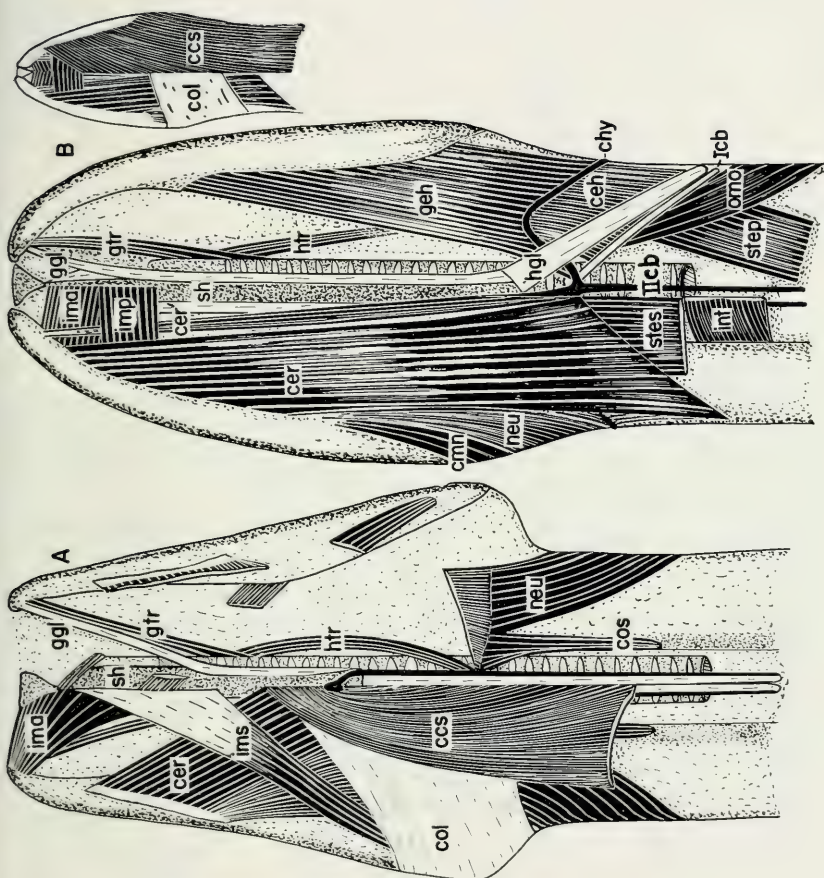
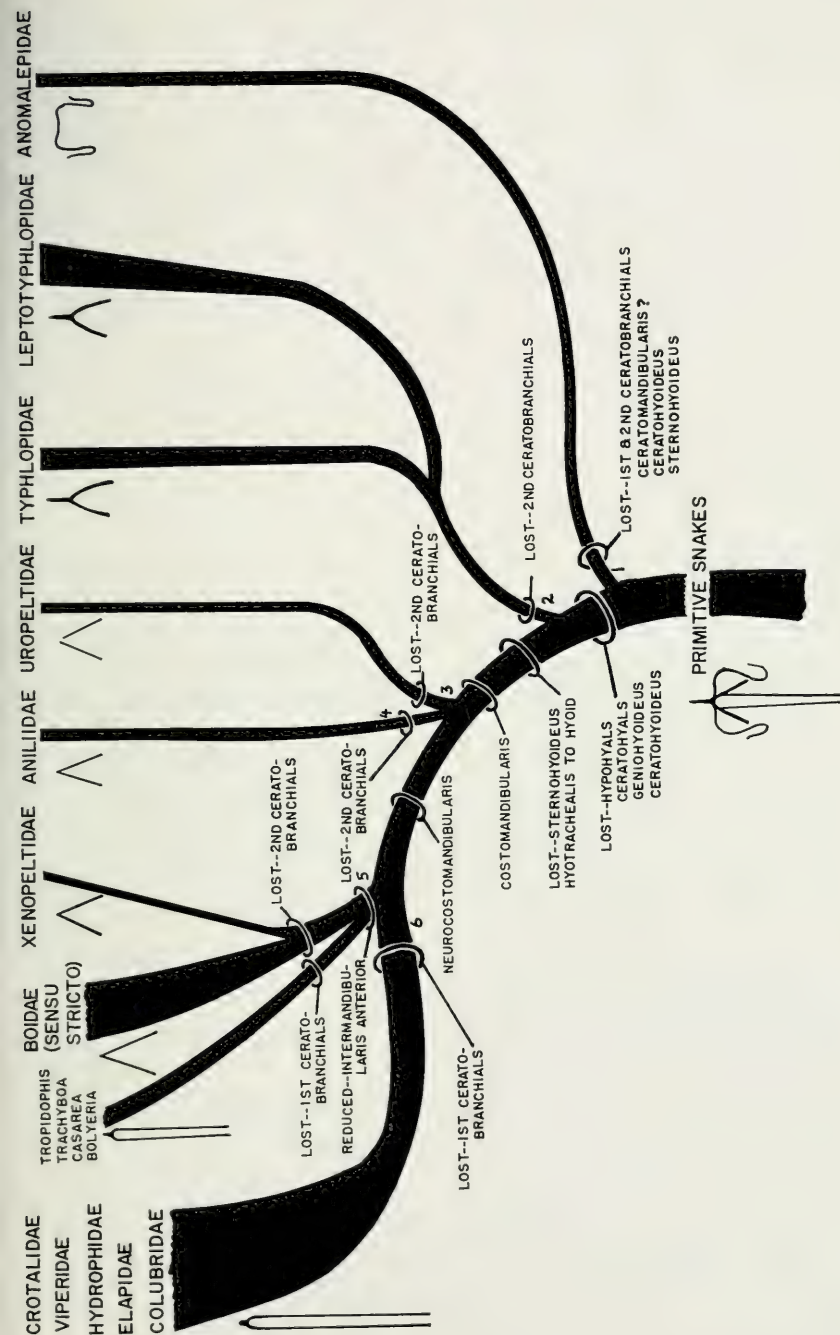


FIGURE 19. A diagram of a phylogenetic arrangement of the present-day families of snakes which has been derived from the study of the hyoid apparatus and its associated musculature. The diagram is also based on an assumption of a monophyletic origin for snakes.

This diagram does not try to give a true relative picture of the possible relationships of the various lines of evolution. For example, the black lines merely indicate in a roughly relative way the numbers of genera and species composing each family, and the vertical, or temporal, scale has no actual definition.

Major events concerning the evolution of the hyoid and its musculature are indicated by the rings along the main trunk and the offshoots. The six lines of evolution which have been derived for the phylogeny of snakes are noted by small numerals at the appropriate places.

Note: for Anomalepididae *read* Anomalepididae.



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